THE GENERA OF MIMOSOIDEAE (LEGUMINOSAE) IN THE SOUTHEASTERN UNITED STATES [1]

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Subfamily MIMOSOIDEAE A. P. de Candolle, Prodromus 2: *tab.* inter 94 & 95, 424. 1825, "Mimoseae"

(MIMOSA SUBFAMILY)

Trees, shrubs, vines, or herbs, often armed with prickles or stipular spines. Leaves alternate, evenly twice pinnate [or rarely once pinnate or modified as phyllodia or scales, or absent], persistent to deciduous, petiolate, the petiole with a conspicuous pulvinus, nectaries present in most genera on petiole and/or rachis, the pinnae usually opposite; leaflets large and few or, more frequently, small and numerous. Inflorescences subterminal, axillary, ramiflorous, or cauliflorous pedunculate spikes, racemes, or heads, the peduncles often fascicled. Flowers mostly small, regular, (3–)5(–7)-merous, perfect, staminate, or sterile (neutral, and then becoming showy in some genera), usually densely clustered, sessile to long-pedicellate, bracteate. Sepals valvate or rarely imbricate in bud, rarely free, usually connate, the lobes usually short. Corolla usually longer than calyx, the petals valvate in bud, free or more usually connate, the lobes long to short, usually exceeding the calyx. Stamens 4–10 (usually as many as or twice as many as corolla lobes) or numerous, free or the filaments connate to form a staminal tube or adnate to corolla, usually exserted; filaments usually white, yellow, pink, or red and often the con-

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spicuous part of the flower; anthers small, basifixed to dorsifixed, often versatile, sometimes with an apical gland; pollen grains shed singly (as monads) or more frequently as compound grains (polyads or pollinia) of 4–64 grains. Gynoecium 1-carpellate [or apocarpous with up to 15 carpels per flower], mostly bilaterally symmetrical, sessile to stipitate, glabrous to pubescent; style usually filiform and slightly exceeding the stamens; stigma terminal, generally minute and concave, or less often dome-shaped; ovary superior, ovules [1 to] many, in two alternating rows along the adaxial suture, hemianatropous to anatropous, obliquely ascending or pendulous, two integumented, crassinucellate. Fruit various, generally a dry to fleshy legume dehiscing along both adaxial and abaxial sutures [rarely explosively] or the adaxial suture dehiscing before the abaxial one, or tardily dehiscent or indehiscent, straight, twisted or variously contorted, continuous within or variously interrupted, or fruit a dry loment. Seeds various, generally plano-compressed, oriented transversely, obliquely, or longitudinally in the fruit, mainly with a leathery to very hard seed coat [or seed coat rarely lacking, the seeds then embedded in a fleshy pulp], often arillate (the aril often fleshy), almost always with a distinct U-shaped line (pleurogram) on each side; endosperm often absent or scarcely developed; embryo minute to large, straight, often with large, flat cotyledons, the radicle generally superior. Embryosac development of the Polygonum type; embryogeny of the Onagrad type. Base chromosome numbers 13, 14. (Mimosaceae R. Br. in Flinders, Voy. Terra Austr. 2: 551. 1814, "Mimoseae," nom. cons.; tribe Mimoseae Bronn, De Formis Pl. Leguminosarum 127, 130. 1822.) TYPE GENUS: *Mimosa* L.

The Mimosoideae is one of three widely recognized subfamilies of the large and important family Leguminosae (Fabaceae). Although some contemporary botanists (e.g., Cronquist, Hutchinson, Takhtajan) treat them as separate families of a single order, the distinguishing characters between the three taxa break down to such a degree that it seems far better to keep them at the rank of subfamily. The Mimosoideae are characterized by actinomorphic (regular) perianth and androecium, by both corolla and calyx valvate in bud (except the calyx imbricate in *Parkia*, *Pentaclethra*, and *Mimozyganthus*), and by seeds usually marked by pleurograms. By contrast, in the Caesalpinioideae the flowers are actinomorphic to zygomorphic, the corolla is imbricate in bud, the calyx usually is imbricate (rarely valvate), and the seeds generally lack pleurograms. The two subfamilies appear to be connected through the caesalpiniaceous genera *Burkea* and *Dimorphandra* and the mimosaceous *Pentaclethra*. The more specialized subfamily Mimosoideae appears to have arisen from the Caesalpinioideae. The relationship between the Mimosoideae and the Faboideae is not so close, the papilionaceous legumes tending, instead, to approach some of the zygomorphic-flowered caesalpiniaceous genera.

A number of artificial assemblages have been established in the Mimosoideae, and it is evident that many of the criteria used to delimit genera are unsatisfactory. Linnaeus placed all the mimosoid legumes known to him (with the exception of *Adenanthera pavonina*) in a single genus, *Mimosa*. In 1805, Willdenow divided *Mimosa* into five genera, and, by 1875, Bentham, in his now classic revision of the subfamily, enumerated six tribes containing 29 genera. Since 1875 generic delimitation has proceeded either toward a reduction in the number of genera (e.g., Kuntze, 1891) or toward the recognition of numerous segregate genera (e.g., Britton & Rose, 1928).

The subfamily Mimosoideae contains approximately 55 to 60 genera distributed throughout tropical, subtropical, and warm-temperate regions of the world. The distribution of species among the 56 genera recognized by Hutchinson (1964) is very uneven. Almost two-thirds of the known species fall into three genera: *Acacia*, with 700–800 species; *Mimosa*, with 400–450 species; and *Inga*, with 350–400 species. Many of the genera are small, and nearly one-half of those recognized by Hutchinson are monotypic. Most of the monotypic ones are African. Obviously, generic lines in this subfamily are in need of a complete re-examination.

Bentham's six tribes (Parkieae, Piptadenieae, Adenanthereae, Eumimoseae [= Mimoseae], Acacieae, and Ingeae) were based mainly on floral and seed characters. Taubert (1894) used the same characteristics in the second major account of the mimosoid legumes. Most authors have maintained these tribes until recently (1964), when both Hutchinson and Schulze-Menz combined the Piptadenieae (endosperm present) with the Adenanthereae (endosperm absent). Both authors also considered the monotypic *Mimozyganthus* Burkart to represent a distinct tribe, Mimozygantheae. Although the tribes recognized by Hutchinson and by Schulze-Menz may have some degree of integrity, they still appear to be largely artificial. For example, the separation of the Mimoseae from the Adenanthereae on the basis of the presence or absence of a gland at the tip of the anther is at best a tenuous distinction (see *Schrankia* and *Desmanthus*). However, considerably more data are needed, especially about the poorly known genera of tropical areas, before more natural infrageneric groupings can be made. Consequently, the genera treated here are assigned to the tribes of Hutchinson and of Schulze-Menz in a very tentative way.

The great variability in the pollen of the Mimosoideae is shown by the occurrence of single grains and several types of compound grains, various aperture systems, and variation in stratification and relief of the pollen exine. The pollen of many genera is shed as single grains (monads), usually tricolporate. Pollen in tetrads is found in *Schrankia* and some species of *Mimosa*, while eight-grained polyads, although infrequent, occur in some species of both *Mimosa* and *Calliandra*. Flattened, disc-shaped, 16-grained polyads are the most frequently encountered of the polyad types (cf. *Acacia*, *Albizia*, *Lysiloma*, and *Pithecellobium* and many species of *Calliandra* and *Inga*). Large 32-grained polyads are found in *Affonsea*, *Samanea*, *Enterolobium*, and some species of *Pithecellobium* and *Inga.* The individual grains of a polyad are often asymmetrical, heteropolar, and 4- to 8-porate.

Sorsa (1969) and Guinet (1969) independently obtained similar data from palynological surveys of the subfamily, but each regarded a different type of pollen as primitive. Guinet considered the tricolporate pollen types to be more complex than the porate ones, while Sorsa contended that the development of the various aperture systems proceeded from colpate and colporate toward the more advanced porate condition. Pollen grains shed individually are isopolar, while those shed as polyads are almost always heteropolar. Guinet linked heteropolarity with the simplest pollen features and isopolarity with the more complex, but Sorsa took the opposite view. Although these differences are unresolved, the many features of the pollen of the Mimosoideae, when correlated with other characteristics, undoubtedly will prove to be very helpful in understanding the complex relationships within this group.

The Mimosoideae are poorly known cytologically, perhaps because of difficulties in obtaining buds at the proper stage of development and because the number of pollen mother cells in an anther is reduced in many genera. The chromosomes are small and have not been studied morphologically. The genera in our range appear to have a base number of 13, except for *Desmanthus* and *Neptunia*, both of which have 14. Polyploids are few but occur in at least *Acacia* and *Mimosa.*

Although variable in size, the seed of members of the Leguminosae generally is compressed, has a large embryo, and a hard but smooth seed coat. Seeds without endosperm occur in all three subfamilies, except in tribes Adenanthereae and Mimoseae of the Mimosoideae. The most distinctive feature of almost all seeeds of the Mimosoideae is the pleurogram (or areole, ligne de suture, lineafisural; see Brenan, Corner) a fine U-shaped groove in the seed coat on each side of the seed. Except for the pleurogram, the significance of which appears to be unknown, the seeds of the Mimosoideae and those of the Caesalpinioideae are very similar.

Leguminous seeds, in general, are long lived, and those of a number of mimosoids have been shown to be remarkable in this respect. Seeds of *Mimosa pudica* have germinated 44 years after collection, *Acacia* after more than 50 years, *Mimosa glomerata* after 81, *Leucaena leucocephala* after 99, and *Albizia Julibrissin* after 50, 70, and 147 years (cf. *Albizia*; under subfamily references see Crocker).

The secondary xylem is either ring porous or diffuse porous, and the mostly solitary vessels are composed of elements with simple perforation plates. Senn (1943) concluded on the basis of the length and configuration of the vessel elements that the Leguminosae are highly specialized. Paratracheal parenchyma is usually abundant in the secondary xylem, except in a few species that have apotracheal parenchyma. The paratracheal parenchyma varies from the simple vasicentric type to confluent or even broadly banded types. Parenchyma patterns of the Mimosoideae are quite similar to those found in the Caesalpinioideae, but patterns in the

Faboideae show considerably more variation than in the other subfamilies.

Septate fibers occur in all three subfamilies, but are most frequent in the Mimosoideae and are very rare in the Faboideae. The occurrence of relatively specialized rays in the secondary wood indicates the advanced nature of the family. Storied rays are absent in the Mimosoideae, infrequent in the Caesalpinioideae, and most frequent in the Faboideae.

The nodal anatomy of the Mimosoideae is of the trilacunar type, with three traces and three gaps. Each of the two lateral traces gives rise to an accessory bundle that supplies one of the stipules. The main vascular supply of the petiole consists of a ring of vascular bundles with accessory bundles found in the adaxial position.

Most mimosoid legumes have extrafloral nectaries on the petiole and/or the rachis of the leaves. These nectaries are generally small, usually cup- or trough-shaped, and secrete a sugar-rich nectar. Some physiologists consider them to be organs for the elimination of waste products or an over-abundance of carbohydrates, but other investigators, mostly naturalists and ecologists, hold that the foliar nectaries entice ants, which, in turn, protect the plant from herbivores. Although the nectaries do indeed attract ants which provide some degree of protection, especially in some tropical species, and there are some remarkable examples of mutualism (see *Acacia*), the available data are inconclusive as to the primary function of these organs. Whatever their function, the many types of foliar nectaries can be useful taxonomically because each type is relatively invariable within a species.

Records of Mimosoideae as fossils, especially those from the southeastern United States, are based almost entirely upon fragments of leaflets. Species of the tropical genera *Inga* and *Pithecellobium* have been reported from deposits of the lower Eocene (Wilcox group) and the middle Eocene (Claiborne group) of the Mississippi Embayment region (Berry, 1916, 1924). The northernmost reported occurrence is *Inga wickliffensis* Berry from Ballard County, Kentucky. The identifications of angiosperms remains from the Mississippi Embayment are being reviewed, and detailed studies of the fragments are beginning to yield more accurate identifications. The presence of *Inga* and *Pithecellobium* in the deposits of the area needs verification.

Species of the Mimosoideae are of less economic importance than those of the Faboideae, but many members of the subfamily are useful. Gum arabic is obtained from *Acacia Senegal* Willd., while tannins are derived from the bark of other acacias, especially from certain species of Australia, South Africa, India, and some regions of the New World. The hard wood of many mimosoid trees is very attractive and takes an excellent polish. Lumber is obtained from species of *Acacia*, *Albizia*, *Xylia*, *Enterolobium*, *Lysiloma*, and many other genera of lesser importance.

The leaves of most mimosoid legumes found in the United States (except those with well-developed spines) are of value as forage for cattle, horses, and some of the larger native mammals. The seeds of all species of our range are eaten by various wildlife, especially birds and rodents. Flowers of some species of *Acacia* and *Leucaena* are prodigious nectar producers and are often important sources of honey. Some of the thicker, fleshier pods (as in species of *Inga*) are used to feed livestock or as an occasional food supplement by the Indians of the lowlands of Central and South America. Many of the small to medium-sized trees with spreading crowns are used as shade trees in coffee- (and to a lesser extent in cacao-) plantations.

Nearly all of the mimosoid legumes grown for their ornamental value are unable to tolerate freezing temperatures and, consequently, can be grown out-of-doors only in southern Florida and southern California. Several species of *Calliandra* are in cultivation, especially the well-known and widely cultivated *C. haematocephala* Hassk., powderpuff tree, and to a lesser extent *C. surinamensis* Bentham. Many species of *Acacia*, especially Australian ones, are cultivated in southern Florida and California for their fragrant and attractive flowers. Occasionally species of *Inga* and *Pithecellobium* are found in cultivation, and the rain tree, *Samanea Saman* (Jacq.) Merr. is grown in southern Florida. Specimens of *Anadenanthera colubrina* (Vell.) Brenan and *Enterolobium cyclocarpum* (Jacq.) Griseb. are in cultivation but are not widely grown.

Representatives of two genera introduced as ornamentals, *Dichrostachys* (DC.) Wight & Arn. and *Adenanthera* L., show signs of becoming naturalized in southern Florida and are, consequently, included in the key that follows. *Dichrostachys cinerea* (L.) Wight & Arn., apparently indigenous to India and Africa, has been introduced into southern Florida from Cuba. Despite the very attractive pink-and-yellow inflorescences, the thorny branches and rampant growth of this shrub or small tree have made it a serious pest in Cuba. Its possible spread in southern Florida should be watched carefully.

The Old World *Adenanthera pavonina* L., red sandalwood, also introduced into the West Indies and Central America, is cultivated as an ornamental tree. The twice-pinnately compound leaves are large with relatively large leaflets, and the valves of the fruits coil and twist upon dehiscence, much like those of *Pithecellobium*, exposing the bright red lens-shaped seeds, which remain attached to the valves. Birds probably serve as effective dispersal agents.

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KEY TO THE GENERA OF MIMOSOIDEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Woody or herbaceous plants with alternate, bipinnately compound leaves usually with one or more nectaries present on the petiole and/or rachis; inflorescences of spikes, heads, or racemes; flowers small, regular, usually 5-merous and perfect or some staminate or infrequently neutral; calyx and corolla small, valvate in aestivation; staminal filaments conspicuous and often showy, 5, 10, or numerous, free or connate; anthers minute; fruit usually a legume or loment, sometimes indehiscent; seeds usually small, with a hard coat and a U-shaped line (pleurogram) on each face.*

A. Stamens 5 or 10.
  B. Plant an unarmed tree; stamens 10.
    C. Inflorescences capitate, axillary; petals free; anthers without an apical gland; pollen shed as single grains; fruit flat, not coiling; seeds compressed, brown. .... 1. *Leucaena.*
    C. Inflorescences racemose, terminal; petals nearly free, united at base; anthers with a deciduous gland at apex; pollen shed in flattened 16-grained polyads; valves of fruit coiling upon dehiscence, persistent,

bearing the brilliant red lens-shaped seeds along the margin. . . . . [*Adenanthera.*]

B. Plant an armed or unarmed shrub, subshrub, or herb; corolla sympetalous (petals distinct or only basally connate in *Desmanthus*); pollen shed as single grains or in tetrads.

D. Flowers pink to white, never yellow; anthers with an apical gland (or this rarely lacking); fruit without a conspicuous stipe.

E. Legume prickly or spinescent; staminal filaments bright pink; pollen in tetrads.

F. Fruit flattened, oblong, the valves separating from the persistent margins and dividing into 1-seeded segments; seeds plano-compressed, ovoid, ovate to orbicular; stems and leaves variously prickly, peduncle of inflorescences unarmed. . . . . 2. *Mimosa.*

F. Fruit tetragonal, splitting into 4 segments; seeds tetragonal to rhomboid; stems, leaves, and peduncles armed with numerous recurved prickles. . . . . 3. *Schrankia.*

E. Legume unarmed, bivalved and splitting along the margin into two segments; staminal filaments light green to white; pollen grains single; plant unarmed. . . . . 4. *Desmanthus.*

D. Flowers, at least the perfect ones, bright yellow, neutral flowers when present with conspicuous yellow, pink, or purplish staminodia; anthers without an apical gland; fruit with or without a conspicuous stipe.

G. Plants perennial, herbaceous, generally prostrate, branchlets unarmed; inflorescences congested spikes; flowers yellow; fruit compressed, not twisting, distinctly stipitate, marginally dehiscent by two valves. . . . . 5. *Neptunia.*

G. Plant woody; branchlets armed; inflorescences elongated spikes; flowers usually yellow and pink; fruit compressed, twisting, lacking a conspicuous stipe, usually indehiscent. . . . [*Dichrostachys.*]

A. Stamens numerous (more than 10); pollen shed in 16-grained, flattened polyads.

H. Stamens usually 50 or more, free. . . . . 6. *Acacia.*

H. Stamens usually 12–50, united at the base or into a distinct tube that generally equals the corolla tube.

I. Fruit dehiscent, the valves separating from the persistent margin; stamens united only at the base; stipules large, becoming foliaceous, deciduous to subpersistent. . . . . 7. *Lysiloma.*

I. Fruit indehiscent or dehiscing along one or both margins, the margin never persistent and separating from the valves; stamens united into a distinct tube; stipules setaceous and caducous or spinescent and persistent.

J. Flowers of an inflorescence dimorphic, the central one or two flowers having an elongated tubular corolla and a long-exserted staminal tube; fruit thin, flattened, membranaceous to chartaceous; seeds without an aril; leaves with many leaflets; branches unarmed. . . . . 8. *Albizia.*

J. Flowers of an inflorescence all alike; fruit usually thick, leathery, coiling; seed arillate; leaves with few leaflets; branches armed or unarmed. . . . . 9. *Pithecellobium.*

Tribe MIMOSEAE Bronn

1. **Leucaena** Bentham, Jour. Bot. Hooker **4**: 416. 1842.

Trees or shrubs of tropical to subtropical habitats; sapwood yellowish, heartwood reddish brown; wood strong, durable, straight-grained; branches unarmed, slender to stout. Leaves persistent, with numerous pairs of pinnae and small leaflets [or with few pinnae and larger leaflets borne in pairs], petiolate, a petiolar nectary often present below the lowest pair of pinnae; stipules minute and caducous or becoming spinescent and persistent. Inflorescences of many-flowered, globose heads, the peduncles axillary, often fascicled or in terminal racemes. Flowers usually perfect, 5-merous, sessile or short-pedicellate, white; subtending bracts small, peltate, usually villous at the apex. Calyx campanulate to tubular, with 5 small lobes. Petals 5, free, narrowly obovate, acute to rounded at apex, narrowing at base, pubescent to glabrous. Stamens 10, free, attached at base of ovary, exserted; filaments filiform; anthers introrse, oblong, pilose [to glabrous], eglandular [rarely glandular], versatile; pollen generally shed as 3-colporate grains [or rarely in 16–28-grained polyads]. Stigma terminal, minute, invaginated and concave; style filiform; ovary stipitate, ovules numerous, anatropous. Legume many-seeded, stipitate, broadly to narrowly plano-compressed, linear-oblong to oblong, dehiscent, the valves thickened on the margins, continuous within, often pubescent when young, glabrous at maturity, the outer pericarp thin and papery, dark-colored, the inner thicker, woody, pale brown. Seeds ovate to obovoid, compressed, transversely oriented, suspended on a long slender funiculus; seed coat thin, crustaceous, brown and lustrous, with a distinct pleurogram; embryo inclosed by a thin horny endosperm; radicle slightly exserted. Base chromosome number 13. (*Ryncholeucaena* Britton & Rose; *Caudoleucaena* Britton & Rose). LECTOTYPE SPECIES: *L. glauca* sensu Bentham [2] (*Mimosa glauca* sensu L., 1763, non 1753) = *L. leucocephala* (Lam.) De Wit; see Britton, N. Am. Trees 526. 1908; Wilbur, Taxon 14: 246. 1965. (Name from Greek *leukos*, white, in reference to the color of the flowers.) — LEADTREE.

A genus of approximately 40 species distributed mainly in Central America, northern South America, and the West Indies. The Polynesian *Leucaena Forsteri* Bentham is better placed in the genus *Schleinitzia*. Three species occur in the United States: two are restricted to Texas, and the third occurs in California, Texas, and, in our range in southern Florida.

A small spreading tree, *Leucaena leucocephala* (Lam.) De Wit [3] (*L.*

[2] Isely (1970) has revived Williams's argument (1964) for selecting *L. diversifolia* as the lectotype species and for rejecting *L. glauca*. Williams holds that "If *Leucaena* is typified by *Mimosa glauca* L. then it will become a generic synonym of *Mimosa*." This argument is untenable as is clearly stated by Art. 10, ICBN, 1972. It is the species that Bentham had (not the name of that species) that is the type of the name *Leucaena*. There is no question about the identity of the species; he merely had the wrong name for it.

[3] Drs. William T. Gillis and William T. Stearn have reached still another conclusion

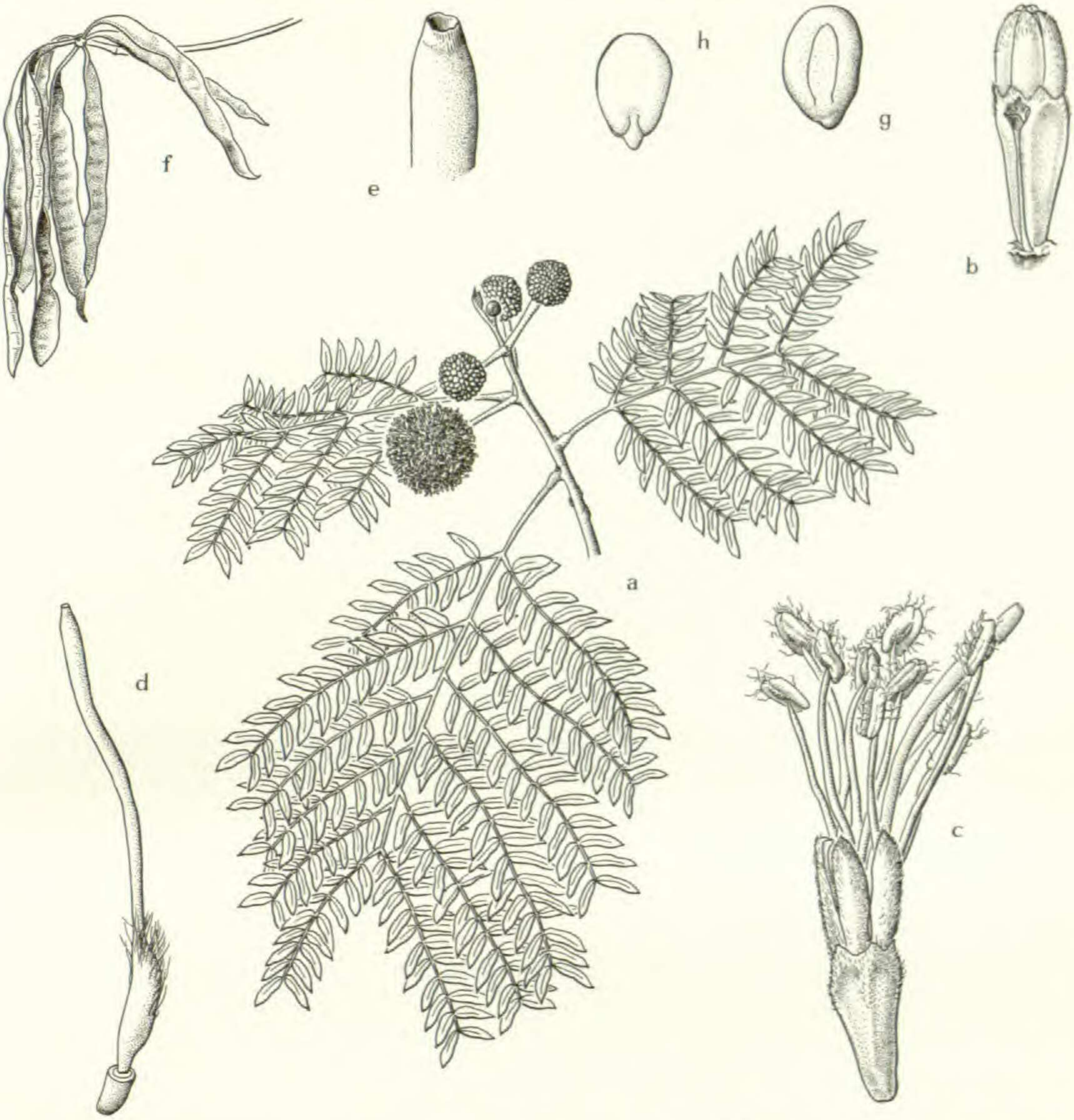

FIGURE 1. **Leucaena.** a–h, *L. leucocephala*: a, branchlet with inflorescences in bud and at anthesis, × 1/2; b, bud and subtending bract, × 6; c, perfect flower, showing pilose anthers, × 6; d, gynoecium, showing substipitate ovary, style, and minute stigma, × 6; e, stigma, showing concave, pore-like construction, × 24; f, infructescence, × 1/4; g, seed, showing pleurogram, × 2; h, embryo, showing slightly exserted radicle, × 2.

glauca (L.) Bentham sensu many authors), leadtree, $2n = 26, 104$, is indigenous from northern South America to southern Mexico, the West Indies (including the Bahamas), and possibly southern Florida. It has been introduced into southern Texas, California, Bermuda, and southward to Argentina and Chile. Widespread introduction and subsequent naturalization of *L. leucocephala* in the Old World tropics has also occurred. The unarmed plants of this species (trees or shrubs) are distinguishable from other mimosoid legumes of the southeastern United States by the leaves

about the correct name for this species and are basing a new combination on *Mimosa latisiliqua* L. Their arguments are presented in "Typification of the names of the species of *Leucaena* and *Lysiloma* in the Bahamas" (Taxon, in press).

with several pinna-pairs bearing numerous small leaflets; by the capitate inflorescences borne in a terminal raceme, the free petals, the 10 free stamens, and the eglandular pilose anthers; and by the legume with valves that separate along both margins but do not recurve.

The individual inflorescences comprising the flowering raceme develop acropetally. The flowers of a single inflorescence are largely synchronous in anthesis and are short lived, generally opening in the morning and remaining open until the following day when they show signs of wilting. The next higher inflorescence usually comes into flower as its predecessor fades. Since a raceme may bear 20–30 inflorescences, the time of flowering can be spread over two or three weeks. The ability of this species to invade cleared areas quickly and successfully is indicative of both its reproductive success and its competitiveness. In Puerto Rico flowering and fruiting have been reported throughout the year, with individual trees of *L. leucocephala* producing large numbers of fruit and viable seeds. In Central America mature plants of *L. leucocephala* are scattered, with relatively few seedlings, and they do not occur in dense stands (Janzen, 1970). Janzen reports that upwards of 90 per cent of the seed crop produced in Central America is lost to bruchid beetle predation. In Puerto Rico, however, bruchid attacks are less frequent, and most of the large number of seeds produced each year are viable, thus accounting for the dense stands. It is theorized that plant species invading islands may leave their predators and parasites behind. If this is so, *L. leucocephala* is a Central American species that has successfully invaded first the West Indies, and then Florida.

Two distinct types of pollen occur in *Leucaena* (Sorsa). In most species the grains are 3-colporate, subspheroidal, medium sized, with an exine 2–4 μm. thick, and are shed as single grains (monads). In a few species the pollen is in 16- to 28-grained polyads with the individual grains having 6–8 paraiso- or hetero-polar pores and being rounded pyramidal with a pointed proximal face and with the exine about 1.5–2 μm. thick. Guinet recognized a third type, which he considered to be intermediate, that is, being shed singly but having the characters of a grain found in a polyad. It seems likely that this type resulted from the acetolysis treatment, which separated the polyads into individual grains thus leading to misinterpretation.

The very high chromosome number $2n = 104$ that has been reported several times may be due to somatic polyploidy, a phenomenon known in several genera of this subfamily. The polyploidy is often present in young primary roots but disappears as the roots age.

Leucaena leucocephala is used as shade for coffee and cacao, and it is also used frequently as either a hedge or a living fence. The leaves are used as green fertilizer (Work) or, when dried, as forage for livestock in place of alfalfa. Gnatt concluded that *L. leucocephala* is superior to common grades of alfalfa meal, and the leaves were shown by Henke to be high in protein content. It has, however, been known for a long time that when moderate to large quantities of the leaves and legumes are eaten by horses, donkeys, mules, and hogs, the animals seem to be in generally poor condition and lose their hair. From a comparison of the symptoms Arnold attributed this effect to selenium accumulated by the plant from the soil and concentrated in the young leaves and seeds, but the poisonous principle has proved to be mimosine, an alpha-amino acid. Conflicting results with feeding experiments in various tropical areas suggest that there may be geographical genetic variation in the amount of mimosine produced by the plant. A recent account of *L. leucocephala* in cultivation is given by Oakes.

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2. **Mimosa** L. Sp. Pl. 1: 516. 1753; Gen. Pl. ed. 5. 233. 1754.

Perennial or rarely annual herbs, shrubs [or rarely trees, sometimes climbing or prostrate], mostly armed with prickles. Leaves bipinnate (in some species with very short rachides, the pinnae appearing digitate) [rarely absent or reduced to phyllodes], often sensitive, petiolar nectaries absent [or rarely present], secondary rachides mostly 2-stipellate, the pinnae with few to numerous leaflets; stipules usually small and subulate, never spinescent. Inflorescences of spikes, racemes or ovoid globose heads, pedunculate, the peduncles solitary or more often fascicled, axillary, ebracteate. Flowers small, sessile, generally perfect, andromonoecious [or sterile in some species with the staminodia becoming subpetaloid at the apex]; perianth (3–)4–5(–6)-merous. Calyx usually minute, gamosepalous, sometimes paleaceous, with small lobes, ciliate [or irregularly laciniate]. Corolla sympetalous, tubular, the lobes often short, pubescent. Stamens the same number as or twice as many as the petals, free, exserted; anthers minute, dorsifixed, introrse, eglandular; pollen shed in tetrads [octads, or in a few species 12-grained polyads.] Stigma in a minute terminal pore; style filiform, usually exceeding the stamens; ovary generally short and sessile, ovules 2 to many. Fruit oblong to linear, usually plano-compressed, straight or curved, sometimes contorted, membranaceous to coriaceous, indehiscent or dehiscent, valves two, separating from the persistent margins, divided transversely into 1-seeded segments (or rarely entire), continuous or subseptate within, often pubescent and armed with prickles. Seeds ovoid, ovate to orbicular, plano-compressed, seed coat hard, lustrous, with a distinct pleurogram, generally transverse, endosperm present; embryo straight, the cotyledons flat. Base chromosome number probably 13. (*Lomoplis* Raf., *Sensitiva* Raf., *Pteromimosa* Britton, *Neomimosa* Britton & Rose, *Mimosopsis* Britton & Rose, *Acanthopteron* Britton, *Haitimimosa* Britton). LECTOTYPE SPECIES: *M. sensitiva* L.; see Britton & Millspaugh, Bahama Flora 161. 1920. (Name from Latin, *mimus*, a mimic, from the sensitive leaves that imitate the movement of an animal [cf. Tournefort, Inst. Rei Herb. 1: 606. 1700, "Mimosa a mimo, cujus motus imitari videtur] or, according to Greene, derived from Spanish *yerba mimosa*, sensitive plant, the name given it by C. Acosta, the first European to write about it [1578].)

A genus of some 400 to 450 species, mainly of South America, but of pantropical distribution and with a few species in mild-temperate regions of the world. The genus has two principal areas of diversification, the main one extending from the grasslands of southern Brazil southward, and the second from the drier grasslands or scrub vegetation in Mexico north into the southwestern United States. A few species of *Mimosa* occur throughout northern South America and Central America. Fifty-six species of *Mimosa* were recorded from Argentina by Burkart (1948) as compared to ten species of *Mimosa* in Texas (Correll & Johnston, 1970). On the basis of number of stamens per flower, *Mimosa* can be divided into two sections, one, or perhaps both, represented in our range by one species.

Section HABBASIA DC. (sect. *Bataucaulo* DC., sect. *Ameria* Bentham), distributed in both hemispheres, is distinguished by flowers with twice as many stamens as petals. Most species of this section shed their pollen grains in 8- or 16-grained polyads, although in some (e.g., *M. strigillosa*) the pollen is in tetrads. Section HABBASIA is represented in the southeastern United States by *M. strigillosa* Torrey & Gray, a native perennial herb that occurs from Florida and Georgia to southern Arkansas, Oklahoma, eastern and southeastern Texas, and Tamaulipas. It is disjunct in Argentina. It is found in meadows, woodlands, hammocks, pinelands and clearings, generally on sandy soils. In addition to the sectional characters, *M. strigillosa* can be recognized by the leaves with 4–8 pairs of pinnae, the peduncles as long as or longer than the leaves, the fruits uniformly spinescent-bristly and not strongly constricted between the seeds.

Section MIMOSA (sect. *Eumimosa* DC.), characterized by flowers with the same number of stamens as petals (generally 4) and restricted to the New World, includes approximately half of the known species of *Mimosa*. Although incompletely sampled, species of this section appear to shed their pollen in tetrads. Section MIMOSA includes the common neotropical *M. pudica* L., sensitive plant, $2n = 52$, which has been introduced as a greenhouse plant in the United States and is possibly incipiently naturalized in the southernmost part of our range. Small reported *M. pudica* as occurring on the Coastal Plain from Florida to Texas, but the lack of verified herbarium specimens fails to support his assertion (see also Ward). *Mimosa pudica* is native to South and Central America and the West Indies, and it has apparently been introduced in many parts of the tropics, presumably for the novelty of the sensitive leaves.

In tropical America, the pink-flowered *Mimosa pudica* can be found in such disturbed situations as roadsides and abandoned fields. It is easily distinguished from *M. strigillosa* by its annual habit and by leaves with one to two pairs of subdigitately arranged pinnae, peduncles shorter than the leaves, stamens as many as the corolla lobes, and fruits strongly constricted between the seeds and with spinescent bristles on the margin.

The leaves of *Mimosa pudica*, as well as most, if not all, other legumes, are nyctinastic, the leaflets folding together at night and the entire leaf dropping from a near horizontal to a more vertical position. The leaves are also sensitive to touch and various other stimuli, the same sort of movement often occurring quite rapidly. In both nyctinastic and thigmonastic responses movement is brought about by differential changes in the volume (turgidity) of motor cells in the pulvinus and the pulvinules. Differences in turgidity between the cells of the upper (adaxial) half of the pulvinus and those of the lower (abaxial) half create tensions in the tissues that, in turn, cause movement. As with *Albizia* (*q.v.*), which is not sensitive to touch, light-dark transition, endogenous circadian rhythms, and phytochrome seem to be involved in the nyctinastic movements. Fondeville *et al.* showed that leaflet-closure is controlled by phytochrome and is evident as few as five minutes after irradiation with red or far-red light. It has been proposed that phytochrome controls membrane properties, and it has been shown that the photoreceptor is in the pulvinus and the pulvinules. Fondeville *et al.* found that the action spectrum for the opening response was most effective in the 710 and 480 nm. ranges, which is similar to the action spectrum for high-energy response affecting morphogenesis in many plants. It appears that a second, as yet unknown pigment (or pigments) is involved.

The rapid response to touch is incompletely understood, but membrane permeability undoubtedly is involved, and, as in nyctinastic responses in *Albizia*, leaflet movement is associated with potassium flux into and out of the motor cells (see Satter & Galston). Calcium flux has been reported during thigmonastic movement in *Mimosa pudica* (Toriyama & Jaffe). The motor cells have many small vacuoles that disappear as cell volume decreases and reappear as turgidity is regained. Some of the vacuoles contain tannin deposits that are reported to have a regulatory function in both thigmonastic (Toriyama & Jaffe) and phytochrome-controlled (Setty & Jaffe) leaflet movements. The actual triggering mechanism of thigmonastic responses has not been accurately determined, but the rapidity of the response indicates that the system depends upon membrane permeability, rather than on enzyme action or gene activation, both of which would elicit slower reactions.

The palynological studies of Sorsa and of Guinet have firmly established the occurrence of three main pollen types in *Mimosa*. In the first, the tetrads of grains range in size from 6.3 μm. to 27μm. on the long axis of the tetrad. In the second common type, the pollen is shed in octads ranging in size from 11.5 μm. to 30 μm. on the long axis of the polyad. The third type, 12-grained polyads, is known in only a few species (perhaps confined to sect. HABBASIA); the polyad varies from 13.8 μm. to 20 μm. on the long axis. The individual grains of the tetrads, octads, and polyads are 3- to 6-porate or the apertures are indistinct. It is notable that *Mimosa* species have the smallest tetrads known in the Leguminosae.

Very little is known about the floral biology and breeding systems of species of *Mimosa*. Although outbreeding is suspected because the pollen is in polyads, self pollination apparently occurs in several species. Circumstantial evidence for self pollination is the lack of floral nectaries in species investigated by Ancibor (1969). Unlike certain species of *Albizia*, *Calliandra*, and *Neptunia*, most or all of the flowers of an inflorescence are generally perfect and capable of producing fruit.

The genus is poorly known cytologically. Chromosome numbers have been reported for only about two per cent of the species. According to Bolkhovskikh *et al.* (1969), six species have $2n = 26$, three species $2n = 52$, one species $2n = 28$, and one $2n = 40$.

Although of limited importance, species of *Mimosa*, when abundant, provide food for wildlife. The leaves are good forage, but the spines deter larger mammals from grazing. The pods and seeds are used by small mammals and by birds, especially quail. The bark is used locally in some regions of Mexico in tanning skins. Because of the short, often branched growth habit of the plants, the wood is not used to any extent in construction or for implements, but is an excellent fuel. The delicate appearance of the bipinnately compound leaves, together with the fragrant flowers makes some species desirable as ornamentals in warm, semiarid regions.

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3. **Schrankia** Willdenow, Linn. Sp. Pl. ed. 4. **4**: 1041. 1806, nom. cons.

Perennial herbs or undershrubs, often prostrate or decumbent, subscandent, or weakly ascending; branches terete to conspicuously angulate, often sulcate, armed with numerous short, recurved, internodal prickles. Leaves usually deciduous, with 1–8 pairs of pinnae, the pinnae when numerous with small leaflets and when few with larger leaflets, the rachis angulate, prickly eglandular, glabrous; leaflets generally small, subsessile to sessile, asymmetrical; stipules subulate, usually setaceous. Inflorescences pedunculate congested spikes or globose heads, axillary, solitary or rarely in pairs. Flowers perfect or polygamous, sessile, pale to bright pink, (4–)5(–6)-parted. Calyx minute, campanulate, with scarcely visible lobes. Corolla tubular to funnel-shaped, connate to about the middle, the lobes narrowly ovate, acute at the apex. Stamens (8–)10(–13), free, long exserted; filaments filiform; anthers minute, eglandular, subdorsifixed; pollen in tetrads. Stigma terminal, minute, invaginated and concave; style filiform; ovary sessile to subsessile, ovules about 16. Fruit linear to narrowly oblong, short to elongate, usually tetragonal, rarely subcompressed, acute to long-acuminate at apex, usually conspicuously prickly (prickles sometimes lacking), nonseptate, dehiscent, both margins splitting away from the sides, producing the effect of four valves. Seeds oriented longitudinally, oblong, subtetragonal to rhomboid, the hilum subapical, the funiculus short; seed coat thick, dark, the pleurogram large, U-shaped; endosperm present; embryo straight. Base chromosome number probably 13. (*Leptoglottis* DC., *Morongia* Britton; not *Schranckia* J. F. Gmelin, 1791, Celastraceae, nom. rejic.) LECTOTYPE SPECIES: *S. aculeata* Willd., nom. illeg. = *Mimosa quadrivalvis* L., *Schrankia quadrivalvis* (L.) Merrill; see ICBN 314. 1972; Isely, Sida **4**: 234. 1971. (Name commemorating Franz von Paula von Schrank, 1747–1835, German botanist and professor of botany at Munich.) — SENSITIVE BRIAR.

A small American genus of perhaps 16–18 species occurring mainly in the southern United States and Mexico, but distributed southward to Argentina. Beard (1963) concluded that all the described species are really a single one that is, in turn, a *Mimosa* (*M. quadrivalvis* L.). Isely (1971) did not accept these arguments and returned to the more traditional concepts within this genus, although he pointed out that problems of specific delimitation still exist.

Turner (1959) treated six species of *Schrankia* in his work on the legumes of Texas, and Isely's account of the genus in the United States closely followed Turner's, although he considered *S. Nuttallii* to be distinct from *S. uncinata*. Four of the seven species recognized by Isely occur in the southeastern United States; *S. Roemeriana* (Scheele) Blankinship and *S. latidens* (Small) Schum. are restricted to Texas and *S. occidentalis* (Wooton & Standley) Standley to Texas and adjoining New

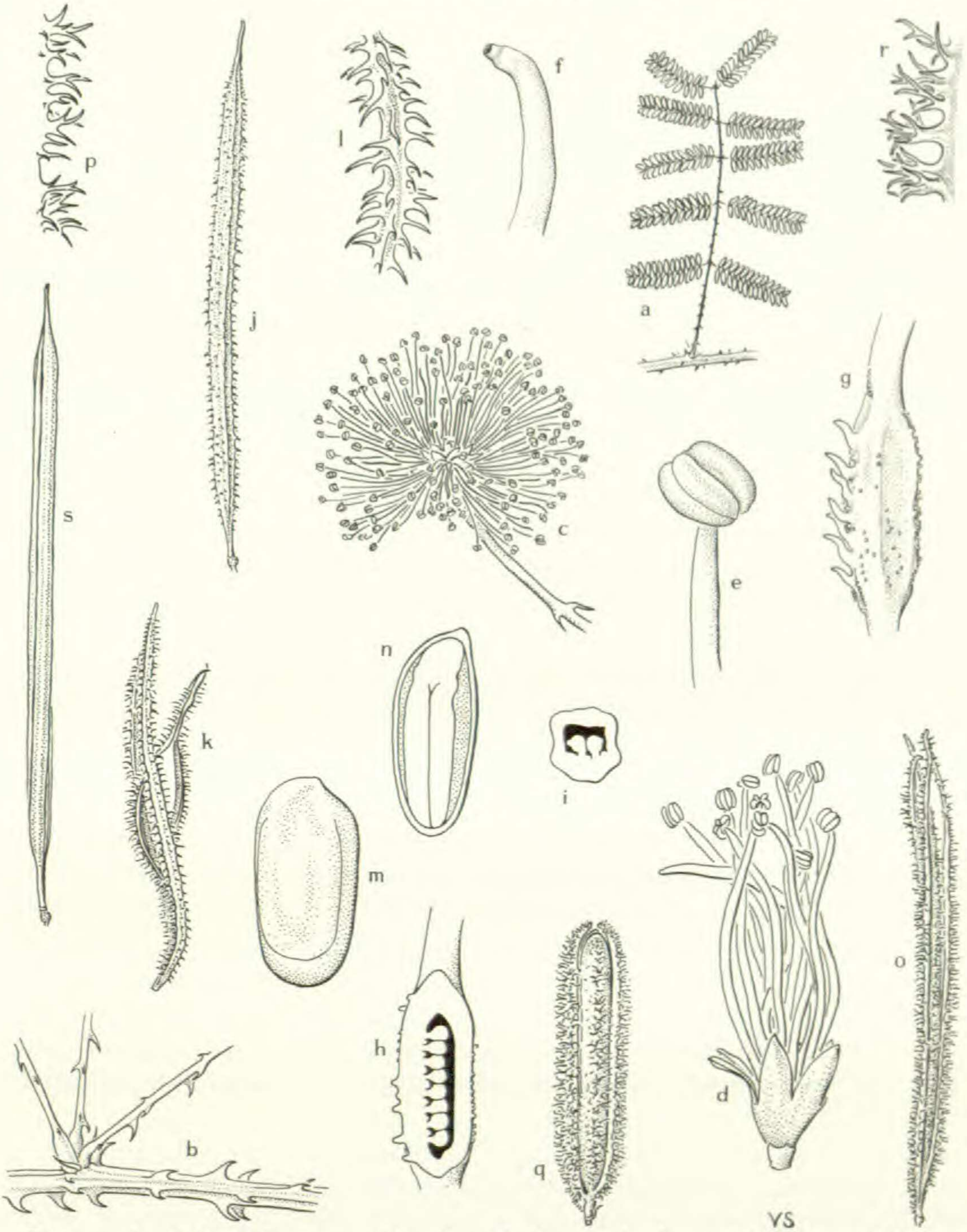

FIGURE 2. **Schrankia.** a–n, *S. microphylla*: a, leaf, × 1/2; b, nodal area, showing petiole (right oblique), two nearly upright peduncles, and the paired stipules, × 2; c, inflorescence at anthesis, × 2; d, perfect flower, × 6; e, anther and upper part of filament, × 20; f, upper part of style terminated by the pore-like stigma, × 20; g, ovary, showing the beginning of development of prickles, × 20; h, ovary, in semidiagrammatic longitudinal section, showing ovules, × 25; i, ovary, in semidiagrammatic cross section, showing ovules in two ranks, × 25; j, mature fruit, × 3/4; k, mature fruit after dehiscence, × 3/4; l, prickles from part of one valve of fruit, × 3; m, seed showing pleurogram, × 6; n, seed, semidiagrammatic longitudinal section, showing cotyledons, radicle and endosperm (stippled), × 6. o, p, *S. Nuttallii*: o, mature fruit at dehiscence, × 3/4; p, prickles on mature fruit, side view, × 3. q, r, *S. hystricina*: q, mature fruit, × 1, r, prickles on mature fruit, side view, × 3. s, *S. uncinata*: mature fruit, extreme form (lacking prickles), × 3/4.

Mexico. The species are often poorly defined, with intergrading forms, and identifications should be made with caution. The present treatment closely follows Turner and Isely.

Restricted to southeastern Texas and southern Louisiana, *Schrankia hystricina* (Small ex Britton & Rose) Standley (*Leptoglottis hystricina* Small ex Britton & Rose), $2n = 26$, is distinguished by leaflets with conspicuously raised reticulate veins on the lower surface, bracts generally longer than the flower buds, a long peduncle, and a short, oblong fruit that is very prickly and rounded at the apex. It occurs in pine or oak woods and in disturbed areas, usually in sandy soils. Flowering is mostly from March through June.

The most widespread species, *Schrankia Nuttallii* (Britton & Rose) Standley (*Leptoglottis Nuttallii* DC. ex Britton & Rose; *S. uncinata* sensu many authors, not Willd.), $2n = 26$, is characterized by leaflets that are strongly reticulate beneath, bracts shorter than the flower buds, peduncles usually shorter than in *S. hystricina*, and an oblong-linear fruit that is densely prickly and tapers at the apex. Isely restricts the range of *S. Nuttallii* to an area from South Dakota to Texas and Louisiana, but Fernald (Gray's Man. Bot. ed. 8) included Alabama and North Carolina. Wilbur (1963) maintains that the Carolinian specimens are *S. microphylla*, an acceptable decision. Although Isely maintains this species as distinct from *S. uncinata* Willd., others (e.g., Turner and Gleason & Cronquist) have reduced *S. Nuttallii* to its synonymy.

Closely related to the two preceding species, *Schrankia uncinata* Willd. (*S. floridana* Chapman) is restricted to an area from southernmost Georgia to central peninsular Florida. It is separated by Isely from the other two species by its leaflets, which are hardly or not at all cuspidate. The fruits are linear-oblong and are very similar to those of *S. Nuttallii*, although they appear to be less prickly. *Schrankia uncinata* also has conspicuously veined leaflets. This species is found in disturbed habitats, pine or scrub woods, especially in sandy soils. It is a poorly known plant, and, until more is known about its biology, its taxonomic status will remain uncertain.

The fourth species in our range, *Schrankia microphylla* (Solander ex Sm.) Macbride[4] (*Mimosa microphylla* Solander ex Sm.; *S. angustata* Torrey & Gray; *Morongia angustata* (Torrey & Gray) Britton; *M. microphylla* (Solander ex Sm.) Britton ex Britton & Brown; *Leptoglottis microphylla* (Solander ex Sm.) Britton & Rose; *L. angustisiliqua* Britton & Rose; *S. angustisiliqua* (Britton & Rose) Hermann), $2n = 16$, lacks the conspicuous leaflet venation and usually has 6–8 pairs of pinnae per leaf. This species has an oblong-linear fruit that is usually very prickly and tapering at the apex. It occurs mainly on the Coastal Plain from southern Virginia to Florida, west to eastern Louisiana and eastern Texas.

Isely concluded that *Schrankia microphylla* includes two variants, al-

[4] Isely (1971) cited this name as *S. microphylla* (Dryander) Macbride, but Britten's arguments (Jour. Bot. **48**: 89, 90. 1920) for citing it as above appear to be correct.

though he did not give them a taxonomic rank. One, consisting of populations throughout the entire range, has shorter fruits that are very prickly and with little or no beak. The second, found only in Florida, is characterized by having four or five pairs of pinnae, smaller leaflets and flower heads, and a linear fruit that is slightly or moderately prickly. The two variant phenotypes intergrade with each other and with the more characteristic ones to form a variable species, the intra- and interspecific limits of which are questionable.

Schrankia is closely related to and probably derived from *Mimosa*. The distinguishing characters are found in the shape of the fruits, and their dehiscence, the shape of the seeds, and the abundance of prickles over most of the plant. The monotypic *Schrankiastrum* Hassler, of Paraguay, is closely allied to both genera and possibly has evolved from some of the highly variable and diverse species of *Mimosa*.

Palynologically *Schrankia* is very similar to *Mimosa*. In both genera the pollen is shed in rhomboidal tetrads. In *Schrankia* the tetrads are approximately 30 μm. in diameter, while in *Mimosa* they range from about 6 to 27 μm. The larger-sized tetrads of *Schrankia* suggest that it is slightly more specialized than *Mimosa*. The individual pollen grains in *Schrankia* are 4–6-porate. The tetrads of the South American *Schrankiastrum insigne* Hassler are approximately 25 μm. in diameter and are almost identical to those found in *Schrankia* and *Mimosa*.

The base chromosome number of *Schrankia* cannot be accurately determined at this time because of the differences in reported numbers. Three species were reported by Turner & Fearing (1960) to have $2n = 26$, while *S. latidens* (Small) Schum. had $2n = 22$. Turner & Beaman (1953) reported $2n = 24$ for *S. occidentalis*. It is not known whether these two instances represent descending aneuploidy. Only *S. leptocarpa* DC., of South America, has been reported to be tetraploid, $2n = 52$. An early report of $2n = 16$ for *S. angustata* (= *S. microphylla*) should be verified. This highly variable assemblage of poorly separated species might be understood better through a thorough cytotaxonomic study.

Data concerning the floral biology and breeding systems are very scanty. Insect pollination is suspected, but self pollination may also occur. Apparently all of the species are sensitive to touch.

Like many of the other genera, *Schrankia* is of no economic importance. The seeds are eaten by small wildlife, especially quail. The leaves are occasionally eaten, but the numerous prickles appear to be an effective deterrent.

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4. **Desmanthus** Willdenow, Linn. Sp. Pl. ed. 4. **4**: 1044. 1806, nom. cons.

Perennial herbs [subshrubs to small trees] of generally dry and often disturbed habitats; branches prostrate to erect, often angulate and striate, glabrous to pubescent, becoming woody, especially at the base, with a large tap root. Leaves with 1 to 15 pairs of pinnae, a nectary usually present between the insertion of the lowest pair of pinnae [rarely with one or more sessile nectaries between the insertion of the upper pairs of pinnae], the rachis angled, glabrous to pubescent, with a setaceous tip; rachis of pinnae narrowly winged, apiculate, the leaflets [4–8] 10–30 pairs per pinna, narrowly linear to oblong, obtuse to acute at the apex, mucronulate, asymmetrical, often ciliolate, glabrous to pubescent, lacking stipels; stipules usually persistent, filiform, setaceous [rarely auriculate]. Inflorescences congested, ovoid to ellipsoid pedunculate spikes, the peduncles solitary and axillary, bracteate. Flowers 5-merous, largely perfect, but the lower flowers of the spike staminate or neutral, or apetalous and with staminodia. Calyx campanulate, with short acute lobes, light green to white. Corolla valvate in aestivation, the petals distinct or connate only at the base, white. Stamens 10 or 5, free, usually exserted; filaments inserted near base of ovary, filiform; anthers bilocular, subdorsifixed, eglandular; pollen shed as 3-colporate or 3-colporoidate single grains. Stigma concave, terminal; style filiform, exceeding the stamens; ovary sessile to subsessile, the ovules numerous. Fruit plano-compressed to subterete, generally linear to oblong, straight to falcate, bivalved, marginally dehiscent, continuous within or subseptate between the seeds. Seeds oriented obliquely to lengthwise in the fruit, ovate to ellipsoid, slightly compressed; embryo inclosed by a horny endosperm; radicle slightly exserted. Base chromosome number 14. (*Acuan* Medicus, 1786, nom. rejic.; *Darlingtonia* DC.; *Acuania* Kuntze). LECTOTYPE SPECIES: *D. virgatus* (L.) Willd. (*Mimosa virgata* L.); Britton & Brown, ed. 2. **2**: 331. 1913; ICBN 314. 1972. (Name from Greek *desme*, a bundle, and *anthos*, flower.)

A small genus of approximately 30 species occurring primarily in tropical and subtropical regions of the New World, a few species largely temperate in distribution. Some 16 species occur in Mexico (Turner, 1950), while nine are reported from Texas (Correll & Johnston). Isely recognized nine species in the United States, three of them in our area.

The herbaceous or suffrutescent *Desmanthus illinoensis* (Michx.) Macmillan ex Robinson & Fern. (*D. brachylobus* (Willd.) Bentham), $2n = 28$, grows in ditches, field margins and open low ground from North Dakota and Minnesota, south to New Mexico and Texas, east to Ohio, and southward to Florida. Its distinguishing characters are the five stamens and the broadly oblong, falcate, and relatively short fruits (ca. 2–5 times as long as broad). The white flowers are first produced from early May to early June, and the plant continues to flower into the summer months. Individual flowers apparently are very short-lived, and the anthers fall within a few hours after the flowers open (Latting). Latting suspects that cross pollination may occur but that selfing is more likely. The legumes, like those of many other genera, are often infested by bruchid beetles. Seeds that are not destroyed by beetles are capable of germinating soon after maturity with no dormancy period required. As in other legumes, the leaves close at night but are not noticeably sensitive to touch.

The more western *Desmanthus leptolobus* Torrey & Gray (*Acuan leptolobum* (Torrey & Gray) Kuntze), $2n = 28$, is reported to occur in our range in Arkansas (Correll & Johnston), its main distribution being from central and southwestern Kansas and southwestern Missouri, south to south-central Texas. Steyermark notes collections from central and eastern Missouri as introductions. Beyond its five stamens per flower, *D. leptolobus* is characterized by few-flowered inflorescences, legumes 5 to 10 times as long as broad and constricted between the seeds, and seeds positioned lengthwise in the fruit. It has adapted to disturbed habitats, such as roadsides and vacant sites, and these may have allowed migration into Missouri and Arkansas. It is also found on calcareous soils, prairies, and sandy or rocky areas.

Our third species, *Desmanthus virgatus* (L.) Willd., $2n = 28$, is widespread in the tropical and subtropical portions of the New World and is naturalized in tropical Asia. It extends into the United States in southern Florida (via the West Indies) and into Texas and Arizona (via Mexico). Its diagnostic features are few-flowered inflorescences, flowers with ten stamens, fruits not constricted between the seeds, seeds oriented obliquely in the fruit, and leaves with relatively few pinnae and with well-developed stipules. Isely recognizes four varieties in the United States. Two occur in Florida: var. *virgatus* (*Acuan texanum* Britton & Rose, *A. Tracyi* Britton & Rose), from the Florida Keys and possibly from Tampa, and the more common var. *depressus* (Willd.) Turner, of southern peninsular Florida and the Keys. According to Isely, var. *virgatus* is an erect or ascending plant in Florida, while var. *depressus* is prostrate or low (in Texas var. *depressus* may also be erect.) The other varieties of the United

States are var. *glandulosus* Turner, of western Texas and adjacent Mexico, and var. *acuminatus* (Benth.) Isely (*D. acuminatus* Benth.), of eastern Texas. The distinctions between the subspecific taxa of *D. virgatus* are at best tenuous and will remain so until a careful biosystematic study of this variable species is made throughout its range.

The strongest relationship of *Desmanthus* is with *Neptunia*. Supporting morphological evidence was given by Windler in his revision of *Neptunia* and this was re-emphasized by Isely. Although Hutchinson places *Desmanthus* in the tribe Mimoseae and *Neptunia* in the tribe Adenanthereae (solely on the presence or absence of glandular anthers) the great similarity of the inflorescences, flowers, fruits, and seeds overwhelmingly supports the placement of these two closely related genera in the same tribe. Additional evidence for their relationship is seen in their pollen, which in both is shed as single grains that are basically 3-colporate, subspheroidal, and medium to large in size. The pollen of *Neptunia* is generally larger than that of *Desmanthus*, has better developed colpi and orae and is occasionally syncolpate or 4-colporate, characters that suggest that *Desmanthus* is perhaps less specialized than *Neptunia*. This interpretation would be further supported by the more specialized inflorescences found in some species of *Neptunia*. Turner & Beaman concluded that *Desmanthus* is more closely related to genera of the Adenanthereae, especially *Dichrostachys*, than to members of the Mimoseae.

Somatic polyploidy has been observed in five species of *Desmanthus* (Turner & Beaman). In all cases the tetraploid cells, $2n = 56$, occurred in the cortical regions of the root tip, while in the undifferentiated apical portion of the root tip only diploid cells, $2n = 28$, were present. According to Bolkhovskikh *et al.* (1969) all six species for which chromosome counts have been reported have $2n = 28$. Most genera of mimosoid legumes have a base chromosome number of 13, but both *Desmanthus* and *Neptunia* have the base number of 14, perhaps a further indication of their close relationship.

Little is known of the biology of the species of *Desmanthus*, except for the study of Latting, who investigated various autecological and biological aspects of *D. illinoensis*. Further studies of this kind are needed for a better understanding of evolutionary relationships within the mimosoid legumes.

The genus is of virtually no economic importance. Graham cited *Desmanthus Cooleyi* (Eaton) Trel. as an erosion-control plant because of its ability to grow on bare areas such as road cuts. The leaves have some forage value, and the seeds have been found in the crops of several species of quail. *Desmanthus illinoensis* was cited similarly.

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5. **Neptunia** Loureiro, Fl. Cochinch. 2: 653. 1790.

Perennial herbs of various habitats [including aquatic], generally with a large tap root, the stems generally prostrate [to ascending], sometimes woody near the base, terete, angulate when young, unbranched to variously branched, glabrous to variously pubescent. Leaves stipulate, with (2–)3–6(–11) pairs of pinnae, petiolar nectaries absent [or 1 or 2 present, sometimes borne at the insertions of the lowest pair of pinnae] the rachis angled, glabrous to pubescent, lacking nectaries [or with small nectaries present between the insertion of each pair of pinnae], the rachis apiculately tipped; rachis of the pinnae distinctly winged, apiculate at tip, the leaflets [6–]8–43 pairs per pinna, oblong, obtuse to broadly acute at the apex, asymmetrical, often ciliolate, glabrous to pubescent; stipules paired, lanceolate to lanceolate-acuminate, obliquely cordate at the base, usually membranaceous, persistent [to deciduous]; stipels [present or] absent. Inflorescences pedunculate congested spikes borne singly or in pairs in leaf axils, usually bracteate, the bracts paired [rarely absent]. Upper flowers perfect; calyx campanulate, 5-merous, sessile, green, rarely yellow; corolla 5-merous, green or yellow; stamens 5 or 10, free, the filaments filiform, attached near the base of the corolla tube, exserted, the anthers bilocular, basifixed, usually terminated by a small stipitate gland, yellow; pollen shed as 3(4)-colporate or occasionally syncolpate monads; stigma concave, terminal, the style filiform, usually exceeding the stamens, the ovary stipitate, ovules many, anatropous. Lower flowers of the spike staminate, calyx campanulate, 5-merous, sessile; corolla 5-merous, yellow; stamens 5 or 10, fertile and like those of the perfect flowers or some or all of them becoming sterile and petaloid; gynoecium lacking. Fruit a legume, plano-compressed, usually oblong, marginally dehiscent by two valves, subseptate between the seeds [or rarely 1-seeded]; seeds transverse, ovate, compressed, funiculus filiform. Base chromosome number 14. (*Hemidesmas* Raf.) TYPE SPECIES: *N. oleracea* Lour. (Name Latin, *Neptunia*, of or belonging to Neptune, god of the sea and other waters, because of the aquatic habit of the type species.)

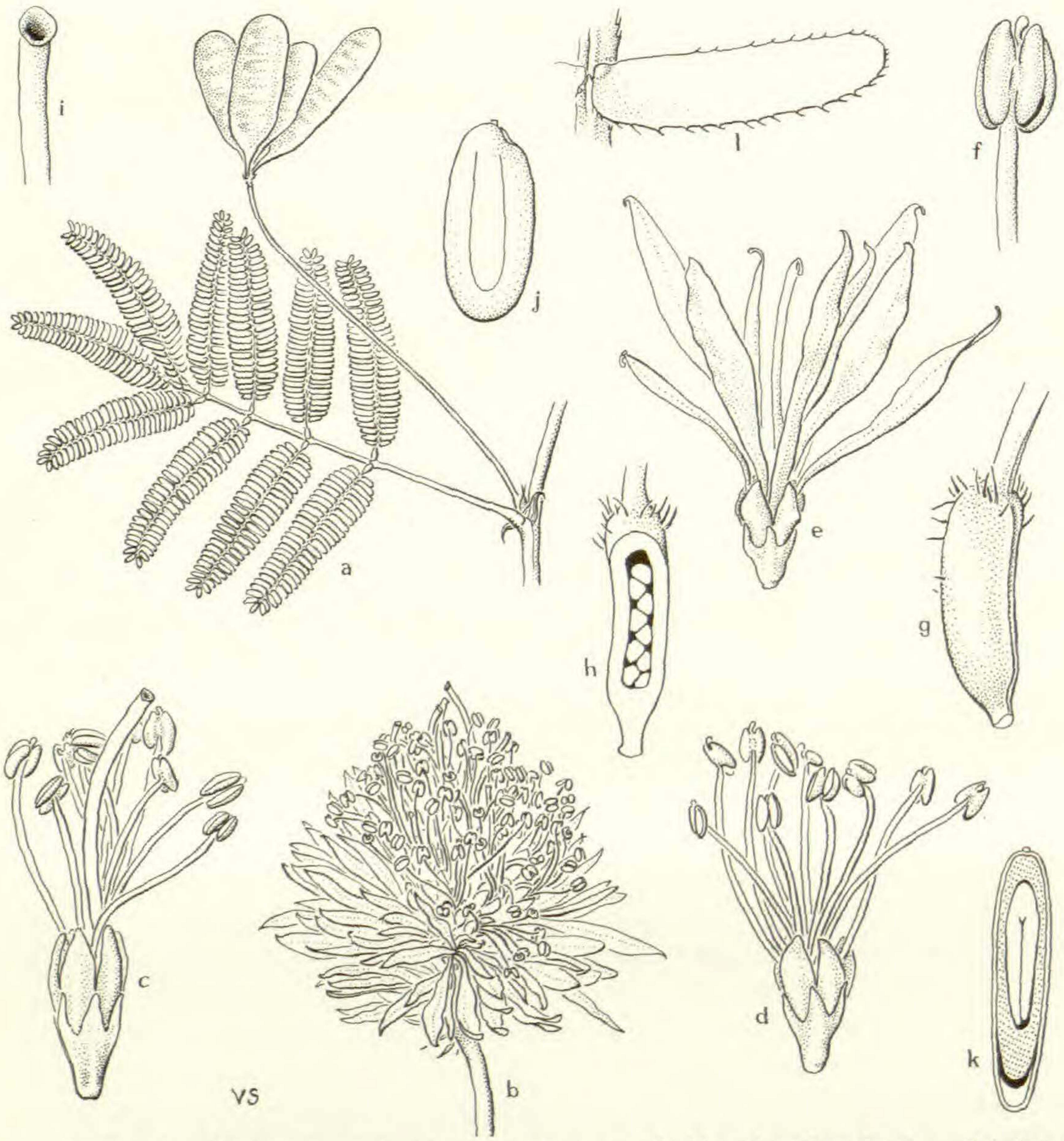

FIGURE 3. **Neptunia.** a–l, *N. pubescens*: a, habit, showing leaf and infructescence, × 1/2; b, inflorescence with perfect flowers at apex, neutral flowers with filaments modified as staminodia below, and staminate flowers in between, × 3; c, perfect flower, × 6; d, staminate flower, × 6; e, neutral flower, showing conspicuous staminodia, × 6; f, anther with apical gland, × 15; g, ovary, × 15; h, ovary in semidiagrammatic longitudinal section, showing the two-ranked ovules, from below, × 15; i, upper part of style showing concave stigma, × 15; j, seed, lateral view showing pleurogram, × 8; k, seed in semidiagrammatic longitudinal section showing embryo and endosperm (stippled), × 8; l, leaflet, × 8.

A small genus of 11 perennial species of tropical to subtropical regions with some penetration into mild temperate areas. Members of the genus are distributed from the southern United States, to Central America, the West Indies, and South America, and in the Old World representatives can be found in tropical Africa, India, southeastern Asia, and most of northern and northeastern Australia. *Neptunia lutea* (Leavenw.) Bentham and *N. pubescens* Bentham, occur in the southeastern United States.

A third species, *N. plena* (L.) Bentham, of coastal areas of Mexico, the West Indies, Central America, northern South America, and tropical Asia, extends into the United States in Texas.

Section NEPTUNIA, characterized by flowers with 10 stamens, occurs in both hemispheres. This section contains six species including the two in our range. The prostrate *Neptunia lutea* (*N. tenuis* Bentham, *N. lutea* var. *multipinnatifida* Turner), $2n = 28$, occurs largely in the eastern halves of Texas and Oklahoma but also extends eastward into Louisiana, Arkansas, southern Mississippi, and Alabama. It appears to be most frequent in fields, prairies, and roadsides. This species is distinguished from *N. pubescens* by the lack of staminodia in the lower flowers of the spike and by the 30- to 60-flowered spike that is cylindrical in bud, the stipules up to 4 mm. long, the fruiting stipe longer than 5 mm., and the white-ciliolate ovary. Although staminodia are lacking, the lower flowers of a spike are functionally staminate. *Neptunia lutea* is the only species of the genus that is endemic to the United States.

The more widespread *Neptunia pubescens* Benth., $2n = 28$, has staminodia present in the lower flowers of a spike, usually fewer than 30 flowers per spike, the spike ellipsoid in bud, the stipules 4–10 mm. long, the fruiting stipe less than 5 mm. long, and the ovary usually glabrous. Varietas *pubescens* (*N. floridana* Small, *N. Lindheimeri* Robinson, *N. pubescens* var. *floridana* (Small) Turner, *N. pubescens* var. *Lindheimeri* (Robinson) Turner), with the fruiting stipe longer than the calyx, the legume tapering toward the stipe and with 3–6 pairs of pinnae per leaf, occurs along the coastal area of the Gulf of Mexico from southern Florida to Mexico and the coastal regions of Central America, in the West Indies, and southward in South America to Argentina. In var. *microcarpa* (Rose) Windler (*N. microcarpa* Rose, *N. Palmeri* Britton & Rose) the fruiting stipe is shorter than the persistent calyx, the legume usually is rounded toward the stipe, and the leaves have 2 or 3 pairs of pinnae. This variety occurs more inland on dry, calcareous soils from southern Texas into Mexico (Coahuila, Nuevo León, Jalisco).

Two species of sect. NEPTUNIA, *N. acinaciformis* (Span.) Miquel and *N. triquetra* (Vahl) Bentham, $2n = 36$, are indigenous to southeastern Asia and India, respectively. The other species of this section, *N. plena* (L.) Bentham, $2n = 78$, and *N. oleracea* Lour. (*N. prostrata* (Lam.) Baillon), $2n = 56$, occur in both hemispheres. An aquatic rarity in the Leguminosae, *N. oleracea* typically has swollen floating stems buoyed by internodal aerenchyma, which Metcalfe (1931) considers homologous with cork, since the aerenchyma cells arise from a phellogen in the same manner as cork cells. The plants, growing in shallow water or near the edges of water, are anchored by a thick tap root, and adventitious roots are produced at the nodes. It seems possible that the aerenchyma may provide aeration for the roots, in addition to being the flotation tissue. The inflorescences, fruits, and most of the leaves extend above the surface of the water. *Neptunia plena* is either terrestrial or aquatic; when aquatic the stems develop aerenchyma, and such plants may be mistaken for

N. oleracea (cf. Fassett). The leaves of at least *N. lutea, N. pubescens, N. plena*, and *N. oleracea* are sensitive to touch.

Section PENTANTHERA Windler is composed of five species that have flowers with only five (rarely three) stamens. Fruit size and seed number per fruit are also reduced. Except for two collections from the Philippines, all five are restricted to Australia. In *N. monosperma* F. Mueller and *N. dimorphantha* Domin the legumes have only one seed (or rarely two). Although these two species are diploids, $2n = 28$, *N. gracilis*, Bentham, also of this section, is reported to be tetraploid, $2n = 56$.

Observations on four species of *Neptunia* show the plants to be self compatible and capable of producing viable seed (Windler). The inflorescences may be nodding, a position that would promote self pollination. Although specific pollinators have not been identified, various flower-visiting insects are suspected. It is not known whether any of the species hybridize or are capable of doing so. In spite of some questionable and conflicting reports, the base chromosome number of the genus appears to be 14, and one or perhaps two polyploid series are present.

Hutchinson's placement of *Neptunia* in the tribe Adenanthereae solely on the basis of stipitate glands on the anthers can hardly be correct, since in at least *N. acinaciformis* and *N. oleracea* the glands are lacking. Field observations to determine whether glands are initially present but are deciduous are obviously desirable. The true affinities of *Neptunia* appear to be with the tribe Mimoseae and *Desmanthus*, the principal difference between the two genera being the orientation of the seeds within the fruit.

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Tribe ACACIEAE Endlicher [5]

6. **Acacia** Miller, Gard. Dict. Abridged Ed. 4. 1: ord. alph. 1754.

Trees or shrubs [sometimes climbers] of various habitats; sapwood generally light in color, distinct or merging with the hard, durable, brownish heartwood, often irregularly grained; branches unarmed or armed with spinescent stipules or infrastipular spines. Leaves often appearing fascicled on short shoots, bipinnate [or modified to phyllodes], persistent or deciduous, petiolate, a nectary usually present on the adaxial side of petiole and/or often present on the rachis at the insertion of the pinnae, each pinna with one to many pairs of usually small, opposite leaflets; stipules small and caducous to large, persistent spines. Inflorescences pedunculate globose heads, pseudoumbels, cylindric spikes, or racemes, solitary and axillary or fasciculate on short leafless shoots and thus appearing paniculate. Flowers largely perfect, the lower flowers of an inflo-

[5] Endlicher (Enchiridion Botanicum 682. 1841) seems to have been the first to use this name at the rank of tribe, and, unfortunately, as a tribal name it appears to be superfluous and illegitimate. In 1834, Wight & Arnott used Acacieae for the name of a subtribe (Prodr. Fl. Penin. Indiae Orient. 1: 267. 1834) that included *Mimosa* L., and Endlicher also recognized this subtribe in his *Genera Plantarum* (p. 1324) in 1840. In 1841, in his *Enchiridion*, Endlicher used Acacieae as a tribe, again including *Mimosa*, which is the type genus of the earlier tribal name Mimoseae Bronn (1822). Although there is no description in the *Enchiridion* and no reference to the earlier *Genera Plantarum* it is impossible to say that there is no connection between the two works by the same author, and one can only say that Endlicher was raising the subtribe to tribal rank. As a subtribal name Acacieae (correctly Acaciinae) is legitimate, but when raised to tribal rank (still including *Mimosa*) it is superfluous and illegitimate. Bentham (London Jour. Bot. 1: 318. 1842) apparently was the first to use Acacieae to include only *Acacia*, and it has mostly been used in that sense to the present. There does not seem to be another tribal name based on any of the segregates of *Acacia*, and there seems to be no way short of conservation tc retain this name as a legitimate one. — C. E. WOOD, JR.

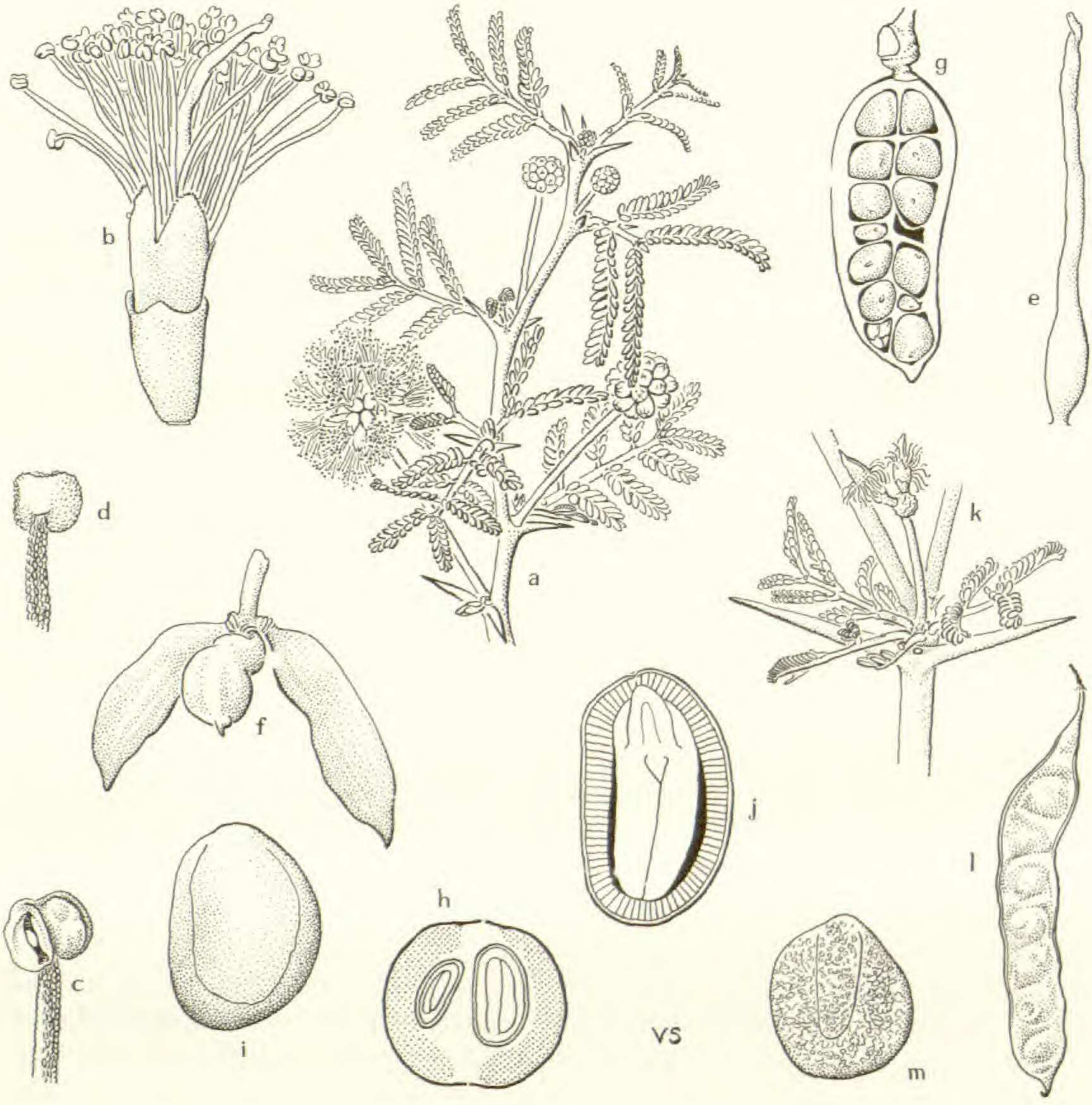

FIGURE 4. **Acacia.** a–k, *A. pinetorum*: a, habit, showing axillary inflorescences, × 2; b, flower, showing numerous stamens and single gynoecium, × 12; c, d, two views of anther, × 40; e, gynoecium, × 12; f, infructescence with three fruits, × 3/4; g, mature fruit with one side removed to show partitions separating seeds, × 1; h, mature fruit in semidiagrammatic cross section showing two seeds slightly superposed, × 2; i, seed, lateral view showing pleurogram, × 4; j, seed in semidiagrammatic longitudinal section showing large embryo and thick seed coat, × 4; k, nodal area showing paired spines, young leaves, and post anthesin inflorescence, × 2. l, m, *A. angustissima*: l, mature fruit, × 3/4; m, seed, lateral view, × 4.

rescence occasionally staminate, (4–)5–6(–7)-merous, sessile to pedicellate; subtending bract small, spathulate to linear and often dilated and peltate at apex, generally caducous. Calyx usually campanulate, with short lobes. Corolla typically funnel shaped, with as many lobes as the calyx, these more or less united [rarely absent]. Stamens usually more than 50, fertile, exserted, free or slightly and irregularly united at base, inserted under or just above base of ovary; filaments filiform; anthers small, eglandular or glandular at apex in some species, dorsifixed, versatile; pollen usually shed in 16- (or less frequently 12-) grained polyads. Stigma minute, terminal; style slender, filiform, exceeding the stamens; ovary elongate, sessile to stipitate, glabrous to puberulous, 1-locular, the ovules numerous. Fruit very variable, compressed, flat, or sometimes cylindric, continuous or moniliform, straight, curved [spiral or contorted], membranaceous to woody, dehiscent or sometimes indehiscent; seeds oriented transversely or longitudinally. Seed generally plano-compressed, usually ovate in outline, without endosperm, with an oval pleurogram on each face; funiculus filiform to thick, variously folded, often surrounding the seed and forming an aril; embryo with flat, oval cotyledons, the radicle straight, included or slightly exserted. Base chromosome number 13. (*Vachellia* Wight & Arn., *Poponax* Raf., *Senegalia* Raf., *Tauroceras* Britton & Rose, *Bahamia* Britton & Rose, *Feracacia* Britton & León, *Lucaya* Britton & Rose, *Fishlockia* Britton & Rose, *Myrmecodendron* Britton & Rose, *Acaciopsis* Britton & Rose; see Hutchinson, 1964, p. 280, for a more complete synonymy.) LECTOTYPE SPECIES: *Acacia vera* [Bauhin] Miller, 1754, nom. invalid. = *Mimosa nilotica* L., *Acacia nilotica* (L.) Delile; see Britton, N. Am. Trees 522. 1908, and Isely, 1969. (Name from Greek, *akakia* [in turn from *akis,* thorn], an Egyptian tree supposedly belonging to this genus.)

The largest genus of the Mimosoideae, with perhaps 700 species very widely distributed in tropical and subtropical regions of the world. Particularly abundant in Australia, the genus also occurs in Africa, southeastern Asia, the Pacific islands, Mexico, South and Central America, the West Indies, and the southern United States. Isely included 15 species in his treatment of the genus in the continental United States, with the largest number of species occurring in Texas. Five or six indigenous species occur in the southeastern United States (all but one in southern Florida), and one or two appear to have escaped from cultivation in Florida.

Bentham (1865) divided *Acacia* into six series based mainly on geographical distribution and on characters of the leaves and the type of inflorescence and its placement. He was unable to use floral or fruiting characters to support these groupings. This classification was adopted by Taubert (1894), and various modifications of the scheme have been used for regional treatments of the genus. The narrow generic concepts used by Britton & Rose (1928) and the resulting segregate genera are highly questionable, the amount of variation found within a single species often being greater than that between the genera established by them. Accordingly, *Acacia* is maintained here in the broad sense.

Of the species of *Acacia* in the southeastern United States, only *A. angustissima* (Miller) Kuntze, $2n = 26$, lacks the glands on petiole or rachis and the stipular spines that are so often associated with the genus. The white to pinkish or yellowish pedicellate flowers are borne in globose heads from summer to fall. The great infraspecific variation in *A. angustissima* has led to a variety of taxonomic treatments, in the most recent of which seven varieties, six of which are represented in the United States, are recognized (Isely). Our representative is var. *hirta* (Nutt. ex Torrey & Gray) Robinson (*Acaciella hirta* (Nutt. ex Torrey & Gray) Britton & Rose), which is an herbaceous to barely suffrutescent plant of prairies, roadsides, open woods, bluffs, and outcrops of shale or limestone from Louisiana and eastern Texas to southern Kansas and Missouri and northern Arkansas. The populations of peninsular Florida apparently are disjunct by several hundred miles. In Isely's circumscription, var. *hirta* intergrades with var. *texensis* (Torrey & Gray) Isely in western Texas. Other variants occur westward to New Mexico and Arizona and southward to Central America. Further study of this complex appears to be needed, since many of the varietal characters seem to be associated with various edaphic factors.

The highly variable *Acacia farnesiana* (L.) Willd. (*Vachellia farnesiana* (L.) Wight & Arn., $2n = 52$, 104, is perhaps the most common and widely distributed species of the genus in the New World. In our range it is primarily a plant of pinelands, hammocks, and disturbed areas, but it extends northward to Tampa and, as an introduction, into southern Georgia (cf. Isely). Beyond the Southeast, it occurs from the West Indies, Mexico, and Central America to South America. It is also found in the Old World, where some occurrences are introductions, while others may possibly be indigenous. The plant is a shrub or a small, spreading tree with generally conspicuous stipular spines, leaves with 4 or 5 pairs of pinnae, leaflets 4–5(–6) mm. long with prominent reticulate venation beneath, and terete obtuse to acute-tipped fruit with the two lateral sutures forming low ridges. The seeds are usually heavily preyed upon by bruchid weevils. There is considerable variation in the development of the stipular spines. The plant is frequently cultivated for its fragrant, bright yellow flowers.

A second species of this complex, *Acacia Smallii* Isely (*Vachellia densiflora* Alexander ex Small) occurs from the western panhandle of Florida to western Texas and sporadically to California and Mexico (fide Isely). A shrub or small tree of scrub areas, roadsides, grasslands, and various disturbed habitats, this plant is characterized by leaflets that are hardly reticulate beneath, by short, stout fruit, and by peduncles that are only 1–1.5 cm. long (*vs.* 2–3 cm. in *A. farnesiana*).

Restricted to southern peninsular Florida and the Keys in our area but perhaps extending into the West Indies, *Acacia pinetorum* Hermann (*Vachellia peninsularis* Small, *V. insularis* Small) is a shrub or small tree found in clearings, coastal scrub vegetation, or pinelands. It is closely related to *A. farnesiana* but can be distinguished by the smaller leaflets that have very obscure or absent lateral veins and by the sharply tapering or beaked fruits that lack protruding sutures. The two species may occur together (e.g., on Big Pine Key, Monroe County), and under these conditions are usually easily distinguished. Some herbarium specimens are difficult to place, however, and further study of the variation in the whole *A. farnesiana* complex is desirable.

The South American *Acacia macracantha* Humb. & Bonpl. ex Willd., $2n = 26$, extends into the West Indies and Mexico and has only recently been reported from Florida. A population on Ramrod Key may possibly be indigenous, but the single tree on Key Vaca (also in Monroe County), which is persistent after cultivation, does not appear to be reproducing. A population on Terra Ceia Island, Manatee County, is spreading from a single old tree that presumably was planted there. This species is distinguished by leaves with 14–20 pairs of pinnae and large, sword-shaped flat stipular spines, by the presence of nectaries between the terminal pair or pairs of pinnae, and by the laterally compressed fruits. (Cf. Ward, 1967, 1968.)

Acacia tortuosa (L.) Willd., $2n = 26$, also discovered recently in Florida, is reported from two localities, both on shell mounds in Collier County (Ward, 1968). As delimited by Isely, this species is West Indian; specimens from Mexico and Texas that have been referred to it are considered by Isely to be *A. Schaffneri* (Watson) Hermann. A small tree with a flat crown, *A. tortuosa* has leaves with 4–8 pairs of pinnae, an inconspicuous nectary present on the rachis between the uppermost pinnae pair, and nearly terete fruits 8–10 cm. long with more or less conspicuous constrictions between the seeds. *Acacia choriophylla* Bentham (*Lucaya choriophylla* (Bentham) Britton & Rose), a plant of the Bahamas and eastern Cuba, has been found wild on Key Largo, Monroe County (cf. Alexander, 1969). This plant is a small, unarmed tree with leaves with minute stipules, 1–3 pairs of pinnae, a nectar gland on the rachis between the two uppermost pinnae pairs, and compressed, oblong, tardily dehiscent legumes.

Ward (1972) has also recorded *Acacia sphaerocephala* Schlecht. & Cham. as sparingly escaped from cultivation in southern Florida. This is one of a Central American group of three to five species of bull-horn or swollen-thorn acacias that includes *A. cornigera* L. Acacias of this group produce leaves the year around and have long-persistent, enlarged, woody stipules with a soft pith, much-enlarged foliar nectaries, and leaflet-, pinna-, and rachis-tips constricted and modified into Beltian bodies. In their native areas, the stipular spines of these plants usually are inhabited by biting and stinging ants of the genus *Pseudomyrmex* that enter the spine by a hole cut near the tip and hollow out the pith. The ants, which live almost entirely on foliar nectar and on the Beltian bodies (a source of protein), attack any other insects on the plant and usually drive them off. They also attack any living plants that touch the foliage of the *Acacia* or that grow below it in an area 10–150 cm. in diameter, so that the acacia grows in a space free from other plants (Janzen).

Approximately 10 per cent of the species of *Acacia* have been investigated cytologically, and several levels of polyploidy have been found. Most of the species for which chromosome numbers have been reported have $2n = 26$, but there are several with $2n = 52$ and $2n = 104$. Sharma & Bhattacharyya investigated the structure and behavior of chromosomes in some species and suggested that polyploidy originated by allopolyploidy.

The inflorescences of *Acacia* are either globose or cylindrical, and the flowers are of varying shades of yellow to orange, rarely white, cream, or pinkish. Although the flowers of a single inflorescence are largely synchronous in anthesis, the inflorescences of a compound floral branch are not. The lowermost inflorescence will flower first, followed centrifugally by succeeding inflorescences. The flowers are often very fragrant, and pollination is mainly by insects. The floral and reproductive biology are very poorly known.

The pollen is generally shed in 16-grained polyads, although pollen in units of 32, 12, 8, or 4 grains is also known in the genus. The polyads are usually radially symmetrical, flattened, and are mostly 40–50 μm. across, although there are occasional species with polyads 90 μm. in diameter and others with polyads as small as 30. Guinet has proposed that *Acacia*, sensu lato, be divided into three large genera based on the number of pores, presence or absence and nature of the individual pollen grain furrows, and the presence or absence of stipular spines. The pores of the individual grains are paraisopolar and may be indistinct. The shape of the grains is variable, but most are pyramidal or cuboidal. In a comparison of 28 South African species with 31 from Australia, Coetzee found that the two groups could easily be separated on the basis of furrow configuration in the exine of the polyads. Within the South African group, the pollen fell into two categories that were somewhat correlated with the type of inflorescence (capitate *vs.* spicate or racemose).

Many species of *Acacia* are cultivated in the United States in greenhouses or in the Southwestern States (including California) and in southern Florida. The majority of the species in cultivation have been introduced from Australia and have leaves that are reduced to phyllodes in the mature plant; compound leaves are produced immediately after the cotyledons in seedlings. One of the most commonly cultivated species is *A. auriculiformis* Cunn., which in southern Florida shows signs of escaping to pine-palmetto woodland.

Species beyond our range are the source of valuable gums, tannins, and dyes. The wood is used locally for firewood and for fence posts. The Australian *A. melanoxylon* R. Br. is used in California as an erosion-control plant on slopes. Various species have been used for hedges and shelterbelts. They provide cover for small wildlife, and the fruits are highly sought after by animals. Deer, horses, and cattle are known to browse on the foliage, bark, and fruit.

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Tribe INGEAE Bentham & Hooker

7. **Lysiloma** Bentham, London Jour. Bot. 3: 82. 1844.

Shrubs or more often trees of moderate to large size, the bark smooth but separating in plate-like scales on older trees, the wood heavy, hard, strong, and close-grained; branches stout, spreading, forming a rounded or flat-topped tree; lenticels numerous, conspicuous. Leaves deciduous [to persistent], pinnae 1 to many pairs, with numerous small leaflets or rarely with few large leaflets, petiolate, a petiolar nectary present just below the lowest pair of pinnae; stipules usually large, foliaceous, deciduous to subpersistent. Inflorescences of pedunculate, many-flowered, globose heads [or cylindrical spikes], solitary or fascicled, usually axillary or terminal. Flowers largely perfect, 5-merous, white, the lower flowers of the inflorescence occasionally staminate, usually sessile. Calyx campanulate [to tubular], the lobes short, equal [to unequal], usually more pubescent than the tube, valvate in aestivation. Corolla tube exceeding the calyx, the lobes approximately 1/4 to 1/3 the length of the tube, ovate, acute at the apex, usually densely pubescent, valvate in aestivation. Stamens generally 12 to 30, united at the base, inserted near the base of the ovary, exserted; filaments filiform; anthers minute, oblong, glabrous, eglandular, peltate; pollen shed in radially symmetric, flattened 16-grained polyads. Stigma terminal, minute, invaginated and concave, style filiform, ovary sessile to short stipitate, ovules numerous. Legume usually 8–12-seeded, straight or slightly falcate, often broad, plano-compressed, oblong, chartaceous, the valves separating at maturity from the persistent margins, continuous within, the exocarp thin, chartaceous, dark colored, separating from the endocarp, the endocarp usually thicker, yellowish. Seeds oriented transversely, plano-compressed, ovate, hard, lustrous, with a small U-shaped pleurogram on each side; funiculus long, slender hilum subbasal; endosperm absent; embryo with flat, oval cotyledons; radicle straight, slightly exserted. Base chromosome number 13. LECTOTYPE SPECIES: *L. bahamense* Bentham; see Britton N. Am. Trees 521. 1908.[6] (Name probably from Greek *lysis*, loose, and *loma*, border, in reference to the separation of valves of the fruit from the persistent margins.)

A small genus of about 35 species distributed in tropical America. Bentham established *Lysiloma* with some reservations (see footnote 6),

[6] Hutchinson (1964, p. 296) argues that *L. bahamense* can not be taken as the type species "because the fruit of that species was unknown to Bentham, who says: 'The generic character lies in the combination of the pod of a *Mimosa* with the monadelphous stamens of the *Ingoid* genera.'" Hutchinson's choice of *L. Schiedeanum,* however, is hardly any better, for Bentham had immature fruit of that species ["Legumen (nondum maturum) 5-pollicare, 8–9 lin. latum, stipitatum, apice longiuscule cuspidatum"], and it appears that he did not have both flowers and mature fruit of *any* of the seven species that he referred to *Lysiloma*. Bentham says, "The species I have collected under this generic name are evidently closely allied to each other, although there can be no certainty of their being truly congeners until the fruit of more species shall be known."

using as the unifying characters the combination of the numerous stamens united to form a tube and the fruit with valves that separate from the persistent margins. Because of its monadelphous stamens, *Lysiloma* has been placed in the tribe Ingeae, within which it is perhaps most closely related to *Albizia*.

Three species, two in the Southwest, occur in the United States. The Mexican *Lysiloma microphyllum* Bentham, which extends into southern Arizona, and *L. Thornberi* Britton & Rose, which is confined to the Rincon Mountains of southern Arizona, have been considered to be conspecific by Isely, who reduced *L. Thornberi* to a variety of *L. microphyllum*. The third, *L. bahamense*, $2n = 26$, is a West Indian species that reaches the United States only in southernmost Florida. It is common on some of the upper Keys and in southernmost peninsular Florida it behaves both as a weed tree and as a component of hammocks (cf. Alexander, Craighead). The tree reaches a maximum of 20 meters. The leaves are deciduous. The small white flowers of an inflorescence can appear from October through June. The fruits ripen by fall but remain on the tree until flowering begins the following year.

Palynologically similar to other mimosoid genera, *Lysiloma* has pollen in 16-grained, flattened symmetrical polyads that range in diameter from 53 to 100 μm. The individual grains are pyramidal in shape, (3–6–)8-porate (fide Sorsa) or 4-porate (fide Guinet), and each circular pore is covered by a membrane.

Data on the floral biology of *Lysiloma* species are almost completely lacking. The conspicuous inflorescences of tiny, fragrant, white flowers suggest cross fertilization by insect pollinators. The size of the polyads may however restrict the effective pollinators to the stronger insects such as bees.

Craighead considers the hammocks of southern Florida to be composed primarily of tropical hardwoods with *Lysiloma bahamense* being one of the more characteristic trees in the hammocks of the Pineland Ridge. Alexander found that in the absence of fire over a twenty-five year period, the pinelands surrounding the hammocks would be invaded by *L. bahamense*, which would persist until another fire at which time the area would revert to a pineland community.

Although the wood is easily worked, durable, and suitable for furniture and interior trim, the trees are generally not very abundant and are often too poorly formed to be of commercial importance as timber. *Lysiloma bahamense* is considered to be a valuable tree in the West Indies, where the wood is used in general construction. Graham listed *L. Thornberi* as a possible erosion-control shrub and roadside ornamental in the southwestern United States.

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8. **Albizia** Durazzini, Magazz. Toscano 3(4) (vol. 12): 10, 13. *pl.* 1772.

Trees or shrubs, small to medium-sized, spreading and often with a flat crown [or large trees]; heartwood pale yellowish brown to brownish, sapwood yellowish; branches unarmed, the branchlets terete to angulate, generally puberulent, becoming glabrate with age, striate. Leaves deciduous; a petiolar nectary usually present; pinnae few to many [a nectary occasionally present between the insertion of each pair of pinnae], with [one to] many pairs of leaflets, the leaflets small and numerous or large and few; stipules usually caducous and setaceous [or rarely large, foliaceous and membranaceous]. Inflorescences of spikes, racemes, or heads, pedunculate, the peduncles solitary or more often fascicled, axillary or generally aggregated on short shoots and appearing paniculate. Flowers largely perfect, (4)5(6)-merous, the lower flowers of the inflorescence often staminate, the central one or two flowers with the corolla tube about 1.5 times longer than the other flowers and the staminal tube exserted, the remaining flowers with the calyx campanulate to short tubular, usually pubescent, short-lobed. Corolla generally infundibuliform, the lobes short (usually about 1/4 the tube length). Stamens 20 to 50, fertile, the filaments united into a staminal tube, the tube included to equalling the corolla tube, inserted near the base of the ovary; filaments filiform; anthers small, eglandular or glandular in bud, peltate; pollen in 16-grained polyads. Stigma terminal, minute, concave; style slender, filiform, slightly exceeding the stamens; ovary elongate, sessile to stipitate, glabrous, 1-locular, ovules ca. 12–18. Legume oblong, flattened, straight, tapering at base and apex, nonseptate, chartaceous to coriaceous, dry, indehiscent to tardily dehiscent, the valves thin, slightly thickened at the margins. Seeds transverse, plano-compressed, hard, lustrous, with a narrow, U-shaped pleurogram on each face, without endosperm; embryo filling the seed cavity, the cotyledons flat, oval, the radicle straight. Base chromosome number 13. (*Sericandra* Raf.) TYPE SPECIES: *A. Julibrissin* Durazz. (Named in honor of "Il Sig. Cavalier Filippo degl' Albizzi," an Italian nobleman who introduced *A. Julibrissin* into Tuscany in 1749. Although the Albizzi family spelled their name with two *z*'s, Durazzini

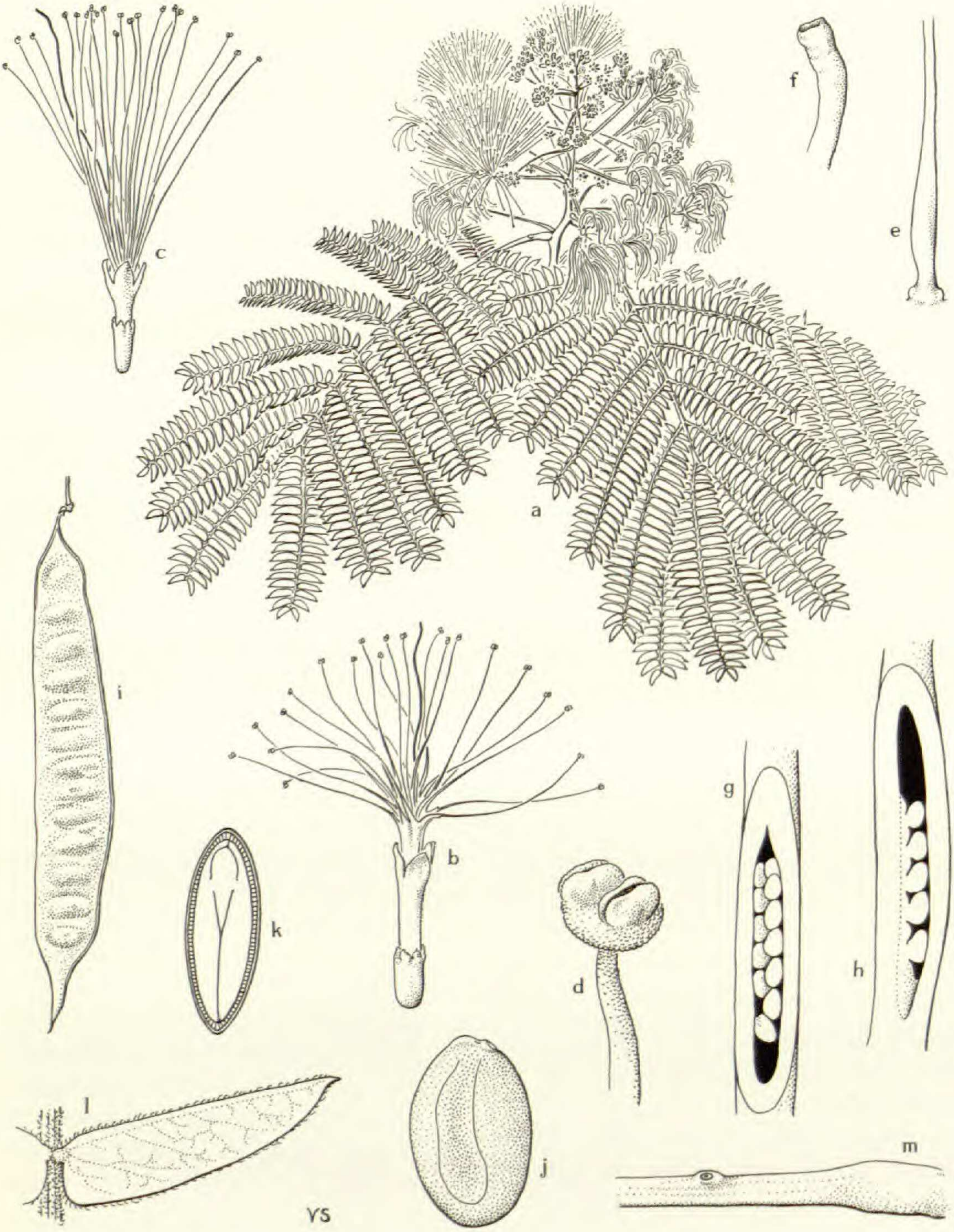

FIGURE 5. **Albizia.** a–l, *A. Julibrissin*: a, habit with compound inflorescence in various stages of flowering, × 1/4; b, perfect central flower of an individual inflorescence showing elongated corolla tube and exserted staminal tube, × 1 1/2; c, nonapical flower of an inflorescence, often functionally staminate, × 1 1/2; d, anther, showing peltate attachment, × 30; e, ovary and lower part of style, × 6; f, upper part of style and terminal concave stigma, × 25; g, ovary in semidiagrammatic longitudinal section from below to show two-ranked ovules, × 20; h, ovary in semidiagrammatic longitudinal section (lateral view) to show ovules, × 20; i, mature fruit, × 1/2; j, seed, lateral view showing pleurogram, × 4; k, seed in semidiagrammatic longitudinal section showing large embryo, × 4; l, leaflet, × 3; m, base of petiole, showing pulvinus and petiolar nectary, × 2.

was consistent in his use of only one in the generic name, and that spelling must be taken as correct. Cf. Little, 1945.)

A genus of approximately a hundred species distributed in tropical and subtropical Asia, Africa, Australia, and the Americas. Fosberg recognized two sections (SPICIFLORAE Bentham and PLATYSPERMAE (Bentham) Fosberg) for Old World species with flowers borne in cylindrical spikes (ca. 15 spp.). (Most previous authors have treated the two together under sect. LOPHANTHA Walpers ex Fournier, a superfluous name.) Section ALBIZIA, with the flowers borne in heads, is represented in both hemispheres, and two species of this section have become naturalized in the southeastern United States.

Native to tropical and subtropical Asia and possibly Africa, *Albizia Lebbeck* (L.) Bentham, $2n = 26$, was introduced first into the West Indies, then into Central and South America, and finally into southern Florida, where it has become naturalized. The tree is medium-sized, with a spreading crown, and is deciduous. The staminal filaments are yellow to white, unlike the pink to reddish ones of *A. Julibrissin.* The rather large fruits, which are produced in prodigious quantities, are long persistent on the tree. As they dry the seeds become loose inside the pods and rattle in a breeze, hence the West Indian vernacular name "woman's tongue." This species can grow in dry areas and in situations of moderate salt spray. It is propagated from seed.

Indigenous to temperate and tropical Asia from Iran to China, Korea, and Japan, *Albizia Julibrissin*, mimosa, silk-tree, $2n = 26$, has long been in cultivation. It has been planted as an ornamental tree throughout most of the eastern United States and over a broad area, from Maryland and West Virginia to Indiana and Kentucky, southward to Louisiana and Florida, has escaped from cultivation, in some areas becoming a conspicuous element along roadsides and woodland margins. It is a small to large flat-topped deciduous tree. The plant flowers from June to mid-September (in New England).

Maturation of the individual inflorescences on a short shoot is acropetal (see FIGURE 5a). Flowering in a single capitate inflorescence is usually more or less synchronous, although the apical flowers generally are the first to reach anthesis. The flowers are short-lived, rarely lasting longer than a day. Relatively few of the 16-grained polyads are produced in each anther, but the transfer of one of these can fertilize most or all of the seeds in a single ovary. The fragrant flowers are visited by numerous insects and by hummingbirds, but bumblebees appear to be the principal pollinators of *A. Julibrissin* in the United States. The upper halves of the filaments are pink to reddish and give the capitate inflorescences their striking "powder-puff" appearance. The plant can be propagated from either seeds or root cuttings.

The leaves of *Albizia Julibrissin* show the "sleep" movements typical of Leguminosae. These movements result from changes in the volume (as much as 3–4-fold) of motor cells in the pulvinus at the base of the petiole, the pulvinus at the base of each pinna, and the pulvinule at the base of each leaflet. Movement is accompanied by potassium flux into and out of the motor cells. Movements are controlled by light-dark transition, phytochrome, and endogenous circadian rhythms. Since it has been shown that the photoreceptors for leaflet movement, the "clock" controlling the rhythmic changes, and the energy substrate (as well as the motor cells) are all located in the pulvini and pulvinules, leaflets of *Albizia Julibrissin* have been used extensively by a number of investigators to study the interaction of these factors. (See Satter & Galston, 1973, for a review and for numerous references; also see *Mimosa*.)

Like those of many other legumes, seeds of *Albizia Julibrissin* are remarkable for their longevity. During an air raid and subsequent fire at the British Museum (Natural History) in 1940 seeds of this species got wet and when examined two months later were found to have germinated after 147 years of storage (Anonymous, 1942). Crocker (1938) notes seeds of this species giving 3.3 per cent germination after 70 years of storage.

At least two other species are known to be under cultivation in the United States. *Albizia Kalkora* (Roxb.) Prain, a small tree with whitish flowers that is native to central and eastern China, Indochina, and India, is only rarely encountered, and *A. lophantha* (Willd.) Bentham, native to Western Australia, is planted in California and Arizona, as well as other warm-temperate (and tropical) parts of the world.

Albizia is questionably distinguished from the other genera of the tribe Ingeae by its thin, straight, flattened fruit that is either indehiscent or tardily dehiscent only along the sutures. It was recognized as a distinct genus by Bentham in both 1844 and in his revision of the subfamily in 1875, but was reduced by Von Mueller (1872) and by Kurz (Jour. Asiat. Soc. Bengal **45**: 129. 1876) to synonymy under *Pithecellobium*. Mohlenbrock placed it between *Havardia* Small (fruits thin, papery, promptly dehiscent) and *Pseudalbizzia* Britton & Rose (fruits indehiscent but breaking transversely between the seeds), both segregates from *Pithecellobium* (q.v.).

Guinet examined the pollen of thirty species of *Albizia* in his survey of the palynology of the Mimosoideae. In all the species the pollen is in flattened, radially symmetrical 16-grained polyads that range in diameter from approximately 65 μm. to 98 μm. The individual pollen grains are 4–6(–8)-porate (the pores usually circular), paraisopolar to heteropolar, and pyramidal in shape.

In a study of the amino acids of the seeds of 29 species of *Albizia* Krauss & Reinbothe separated 36 protein and nonprotein amino acids. Twenty-three contained large amounts of albizzine. *Albizia polyphylla* and *A. polymorpha* were unique in containing mimosine, 5-hydroxypipecolic acid, and dichrosrachic acid.

Beyond the horticultural merits of some species of *Albizia*, notably *A. Julibrissin*, the genus is of limited economic importance. In the Old World some of the species are trees large enough to produce useful timber. The wood of the smaller trees is often used for fuel, fence posts, small furniture, paneling, and general construction. The bark has been used in tanning and for medicinal purposes. It has been used in various decoctions as an anthelmintic.

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9. **Pithecellobium** C. F. P. von Martius, Flora 20(2)(Beibl. 8): 114. 1837,[7] "Pithecollobium," nom. et orth. cons.

Trees or shrubs; bark smooth, often becoming rough in old trees, usually gray; sapwood often pungent, heartwood yellow to brown or almost to black; branches terete to angulate, unarmed or armed with persistent spinescent stipules, the branchlets with conspicuous, small pale lenticels. Leaves bipinnate [or rarely once-pinnate], petiolate [the pulvinus rarely subtended by large nectaries], the pinnae few to many-foliolate, a nectary usually present between the insertion of each pair of pinnae and often between the insertion of each pair of leaflets, the leaflets opposite [although the lower ones tend to be subalternate to alternate, occasionally the inner leaflet of the lowest pair absent]; stipules persistent and becoming spinescent [or large and foliaceous] or early caducous. Inflorescences of oblong spikes or racemes, globose heads, or pseudoumbels, pedunculate, the peduncles in terminal panicles or fascicled and axillary or fascicled and ramiflorous, the bracts minute, generally caducous. Flowers largely perfect [rarely the lower flowers functionally staminate], 5-(6)-merous, sessile to pedicellate. Calyx campanulate, with short lobes, glabrous to variously pubescent. Corolla infundibular, exceeding [or rarely equalling the calyx], the lobes short to long (up to 1/2 the length of the tube). Stamens numerous; filaments united into a tube generally equalling corolla tube, inserted near base of ovary; anthers minute, dorsifixed and versatile, eglandular; pollen in flattened, symmetrical 16-grained polyads. Stigma minute, terminal; style slender, filiform, exceeding stamens; ovary elongate, generally stipitate [rarely reduced or aborted], ovules numerous. Legume straight or curved, flattened to terete, 2-valved, dehiscent [or indehiscent], the valves continuous or interrupted within, dehiscence occurring along both sutures at the same time or proceeding from on the adaxial suture to the abaxial suture (usually incomplete), the valves becoming contorted after dehiscence. Seeds slightly to distinctly plano-compressed, oriented transversely in the fruit, the funiculus filiform or expanded into a conspicuous fleshy aril (in our species the aril red to white and the seeds hanging by the funiculus upon dehiscence of fruit); hilum subbasal; seed coat thick to thin, with a faint oval pleurogram; endosperm lacking, the embryo filling seed cavity, the radicle included or slightly exserted. Base chromosome number 13. (Including *Spiroloba* Raf.; *Siderocarpus* Small, not Pierre, 1888; *Havardia* Small; *Jupunba* Britton & Rose; *Cojoba* Britton & Rose; *Ebenopsis* Britton & Rose; *Painteria* Britton & Rose; *Chloroleucon* (Bentham) Britton & Rose; *Pseudalbizzia* Britton & Rose; *Abarema* Pittier; *Macrosamanea* Britton & Rose; *Klugiodendron* Britton & Rose; *Arthrosamanea* Britton & Rose; *Marmaroxylon* Killip; *Ortholobium* Gagnepain). LECTOTYPE SPECIES:

[7] The initial publication for *Pithecellobium* has often been cited as Martius, Hort. Reg. Monac. 188. 1829, but neither a description nor an illustration is given there. See Rickett & Stafleu, Taxon **8**: 288. 1959.

P. Unguis-cati (L.) Bentham (*Mimosa Unguis-cati* L.), typ. cons.; see ICBN 314. 1972, and Britton, N. Am. Trees 514. 1908. (Name from Greek, *pithekos*, ape, and *ellobion*, earring, from a Brazilian name [given by Martius as *brincos de sahoy*, monkey's earring] for one of the species, apparently in reference to the twisted fruit.)

The genus includes some 90 species distributed in tropical and subtropical habitats in both hemispheres, from southern Florida and Texas, the West Indies, Central and South America, and from tropical Asia, to Malesia and Australia. Of the five species that reach the southern United States, three, all of sect. PITHECELLOBIUM (sect. *Unguis-cati* Bentham), occur in southern Florida. *Pithecellobium flexicaule* (Bentham) Coulter and *P. pallens* (Bentham) Standley extend from Mexico northward into southern Texas. Our species are closely related and, as members of sect. PITHECELLOBIUM are characterized by spinescent stipules (except in *P. guadalupense*), leaves with (1 or) 2 to several pinnae and several pairs of leaflets, fruits with valves that are contorted after dehiscence, and arillate seeds.

A small, flat-topped shrub or tree, *Pithecellobium guadalupense* (Pers.) Chapman (*P. keyense* Britton), $2n = 26$, Guadeloupe blackbead, is characterized by leaves that generally lack spinescent stipules and have persistent, coriaceous, obovate to nearly orbicular leaflets. The pattern of branching is irregular, like that of many other species of the genus. The plant occurs in rocky or sandy soil in pine woods, in hammocks, and on open sand dunes of southern Florida, including the Keys. It is widely distributed in the West Indies and occurs in the Yucatán Peninsula. Flowering usually is from October through March. The flowers are aggregated in dense globose heads that are, in turn, borne in terminal panicles. The pink upper halves of the filaments produce an over-all effect of pink flowers.

A shrub or small tree, *Pithecellobium Unguis-cati*, catclaw blackbead, has angulate branchlets and leaves with stipular spines and persistent, chartaceous, obliquely obovate to oblong leaflets. In our area this species is restricted to southern peninsular Florida, including the Keys; its distribution elsewhere has been difficult to determine because it has been confused with other species, but Little (1953) included the West Indies, Mexico, Central America, and northern South America. As in *P. guadalupense*, the flowers are borne in globose heads, and the filaments give the inflorescences their pinkish to yellow color. The terminal panicle of inflorescences of both these species is more compact than in *P. dulce*. The black seeds of both this and the preceding species have a bright red aril.

The third species, *Pithecellobium dulce* (Roxb.) Bentham (*Mimosa dulcis* Roxb., *Feuilleea dulcis* (Roxb.) Kuntze), $2n = 26$, is a small to medium-sized tree with leaves with stipular spines and persistent, chartaceous to subcoriaceous, strongly oblique oblong leaflets. The whitish heads of flowers are borne on short peduncles in a narrow panicle. The arils of the black seeds are white to pink, acidulous, and edible (cf. Standley). Indigenous from Baja California to northern South America, *P. dulce* is widely planted elsewhere, and it was an early introduction into the Philippines. Lakela & Craighead and Long & Lakela have reported it as occurring in Collier County, Florida, and several presumably wild individuals have been found in Dade County, as well. It is presumably an escape from cultivation in our area.

The generic limits of *Pithecellobium* have been interpreted quite variously. Bentham at first (1844) recognized 75 species in eight sections but he later (1875) placed 108 species in seven sections. Britton & Rose's narrow concept of *Pithecellobium* (1928) led to the description of a number of new genera based mainly on fruit characters, and, to a lesser extent, on the position of the inflorescence. Students of neotropical plants have largely rejected these segregate genera as artificial, but Kostermans (1954) has split the Old World species into 11 genera, describing six of them as new and restricting *Pithecellobium* to the New World. He relied heavily on fruit and seed characters, the presence or absence of spines, and, to a lesser degree, on the position of the inflorescence. Mohlenbrock (1963a, b), employing a broader generic concept, although maintaining a number of the segregates (e.g., *Havardia*, *Pseudalbizzia*), reduced the Old World *Archidendron* to sectional rank under *Pithecellobium* and recognized five additional sections in the genus. In his concept *Pithecellobium* includes all those species in which the valves of the fruit become spirally contorted after dehiscence. Since the splintering of this large and loose assemblage into numerous seemingly artificial segregate genera does not solve the taxonomic problems, it seems better for the present to treat *Pithecellobium* in the broad sense.

Most species of *Pithecellobium* are plants of the margins of forests and waterways in tropical and subtropical areas. They are also found in developing secondary forest. The species found in pioneer vegetation and in unstable habitats typically have dehiscent pods with dangling seeds and conspicuous arils, adaptations for bird dispersal. Species that are restricted to the secondary tree element of mature rain forest usually have indehiscent, somewhat fleshy fruits that are dispersed by mammals. Van der Pijl (1956) has also cited water as a dispersal agent for those species that occur along waterways and that also have dry fruits and seeds that lack an aril. In the three species that occur in the southeastern United States the pods twist and coil in a loose spiral during dehiscence. The seeds have a conspicuous aril, are shiny black, and hang free by the funiculus. The seeds of all three presumably are dispersed by birds (cf. Ridley, 1930; van der Pijl, 1956).

Palynologically, *Pithecellobium* is specialized, with its pollen arranged in flattened, radially symmetrical 16- or 32-grained polyads similar to those of *Inga*, *Affonsea*, *Lysiloma*, and most species of *Calliandra*. The individual grains are usually pyramidal to oval in shape, generally 6–8-porate, and paraisopolar to heteropolar.

Apparently the chromosome numbers of only eight species of *Pithecel-*

lobium have been reported. Seven of these are diploids, $2n = 26$, and *P. polycephalum* is reported to be a tetraploid, $2n = 52$.

The wood is of very limited use, since plants of most species of the genus are small, often much-branched trees. The wood is hard, heavy, and strong, but brittle, and it is used mainly for fence posts and for fuel. The bark yields a yellow dye that has been used in tropical America for tanning skins (Record & Hess, 1943). Record & Hess also report that the bark is used in decoctions for its astringent properties.

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